MOTHER-PUP RECOGNITION BEHAVIOUR, PUP VOCAL SIGNATURES AND ALLOSUCKLING IN THE NEW ZEALAND FUR SEAL, *ARCTOCEPHALUS FORSTERI*

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Abstract

A recognition system is required between pinniped mothers and pups. For otariids this is especially important since females frequently leave their pups for foraging and must reunite on return. Pups must deal with these fasting periods during maternal absence and consequently may attempt to obtain allomaternal care from unrelated females. This research on the New Zealand fur seal (*Arctocephalus forsteri*) at Ohau Point, Kaikoura, New Zealand, quantified mother-pup recognition behaviour during reunions, individuality of pup calls used by mothers to recognise their pup, and the occurrence of allosuckling as a possible recognition error by females and as a strategy employed by pups to gain allomaternal care during their mothers' absence. A combination of behavioural observations, morphometry, VHF radio telemetry, acoustics and DNA genotyping were employed to study these topics. Postpartum interaction behaviours between mothers and pups appeared to facilitate development of an efficient mother-pup recognition system, involving mainly vocal and olfactory cues that were utilised during reunions. Greater selective pressure on pups to reunite resulted in an asymmetry of searching behaviour between females and pups during reunions. The vocalisations of pups were stereotypic, especially those features of the fundamental frequency and frequency of the lowest harmonic, which are likely to facilitate recognition of a pup by their mother. Pups attempted to steal milk from unrelated females more often during maternal absence and appeared to modify the intra-individual variation pattern of a feature of their vocal signatures over this period, which may assist attempts at allosuckling under nutritional stress. Fostering was demonstrated to occur despite costs to filial pups and possible costs to female reproductive success and may be attributed to development of erroneous recognition

between females and non filial pups, or kin selection. This study provides a valuable contribution to the knowledge of recognition systems between pinniped mothers and pups, of alternative pup strategies under nutritional stress and of the rare occurrence of fostering in otariid pinnipeds.

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Chapter 1: General Introduction

Pinniped maternal strategies

The pinnipeds are a unique group of carnivorous mammals that have adapted to both a marine and terrestrial existence. Thirty-three extant species comprise Order Pinnipedia: eighteen phocids (true seals or earless seals), fourteen otariids (fur seals and sea lions, or eared seals) and one odobenid (walrus). Of the phocids, 8 species belong to the subfamily Monachinae or 'southern' phocids, and 10 species to the subfamily Phocinae, or the northern phocids (Riedman, 1990). Likewise the otariids are divided into two subfamilies, the Otariinae or sea lions (5 species), and the subfamily Arctocephalinae or fur seals (9 species).

As in most mammals, parental care in pinnipeds is provided solely by females. Despite spending the majority of time foraging at sea, they require land or ice on which to give birth and nurse their young, with the exception of the walrus (Boness & Bowen, 1996). These circumstances have resulted in the evolution of unusual behavioural and physiological strategies of lactation and maternal care. The general view is that there are three basic strategies characteristic of each pinniped family: 1) fasting in phocids, 2) foraging cycles and aquatic nursing in odobenids, and 3) foraging cycles in otariids (Boness & Bowen, 1996).

Phocids are characterised by a fasting maternal strategy (for an extensive fraction of lactation) and a short lactation period (Gentry & Kooyman, 1986; Riedman, 1990; Boness & Bowen, 1996). Lactation length ranges from 4 days in the hooded seal, *Cystophora cristata*, to 68 days in the Baikal seal, *Phoca sibirica* (Riedman, 1990). In

the pagophillic (ice-breeding) phocids there is a strong selection pressure for a shorter lactation period compared to the land breeding seals. This is because of the instability of pack ice and the unsheltered environment for newborn seals with little insulating blubber. Phocid milk has a much higher fat content than that of otariids and odobenids and pups grow more rapidly (Boness & Bowen, 1996). Additionally, phocid pups are comparatively larger in size and more precocial at birth than otariid and odobenid pups (Riedman, 1990).

Odobenid females feed during lactation and exhibit an extended lactation period of up to three years (Kovacs & Lavigne, 1992). Walrus pups nurse off their mothers at sea and on ice, and begin to go on foraging trips with their mothers at about 5 months of age (Riedman, 1990; Boness & Bowen, 1996).

Otariids have a maternal cycle whereby they alternate nursing bouts with foraging at sea, and have an extended lactation period of around 4 months (northern fur seal, *Callorhinus ursinus* and Antarctic fur seal, *Arctocephalus gazella)* to 12-36 months (Galapágos fur seal, *A. galapagoensis*) (Riedman, 1990). Otariids do not have to contend with problems associated with raising young in unfavourable environments like many phocids, so there is little selective pressure to encourage short lactation periods. The ability to forage while nursing young allows an extended period of lactation (Kovacs & Lavigne, 1992).

It has recently been suggested that the conventional view of three different maternal strategies that correspond with the three families of pinnipeds is overly simplistic (Boness & Bowen, 1996). The maternal foraging cycle seen in all otariids is found in

at least one phocid, the harbour seal (*Phoca vitulina*; Boness *et al*., 1994). Boness *et al*. (1994) found that the majority of female harbour seals began diving by mid-lactation (12 days postpartum) and made an average of seven dives during the remainder of the lactation period. It is suggested that maternal size determines the maternal strategy as harbour seals are among the smallest phocids (Boness *et al*., 1994). Small maternal size constrains the amount of stored energy female seals can bring to the rookery to transfer to their pups, so they are required to begin feeding during lactation (Bowen *et al*., 1987).

New Zealand fur seal breeding biology

The New Zealand fur seal (*Arctocephalus forsteri*), an otariid, breeds on rocky shores of New Zealand, South and Western Australia as well as the Australasian temperate and subantarctic islands (Crawley, 1990). Commercial sealers nearly hunted fur seals to extinction in the 19th century (Wilson, 1992). Legal protection was first given in 1894, and since then they have not been legally harvested except for short open seasons, with the latest in 1946 (Sorensen, 1969), and for scientific research (Crawley & Wilson, 1976). The Marine Mammal Protection Act has fully protected seals since 1978 (Cawthorn *et al*., 1985).

Before exploitation by Polynesians and Europeans, pre-1000 AD fur seal breeding colonies were distributed throughout New Zealand (Taylor *et al*., 1995). By the 20th century the mainland distribution was restricted to South Westland (Wilson, 1992). Protection from exploitation has allowed fur seal numbers to increase, especially in recent years. At present numerous colonies are located around the South Island coastline, with breeding colonies being re-established in the southern-most part of the

North Island (Dix, 1993). Fur seal numbers in New Zealand waters are estimated to be to the order of 100,000 (Taylor *et al*., 1995).

Otariids exhibit a more pronounced sexual bimaturism than phocids (Riedman, 1990). New Zealand fur seal females reach sexual maturity at 2-5 years of age, whereas males are sexually mature at 8-12 years and will not hold a territory until at least 9-10 years of age (Mattlin, 1978a; Riedman, 1990; Crawley, 1990). Like many other otariid pinnipeds, New Zealand fur seals display resource defence polygyny. Males arrive at the colony in October to set up territories before females arrive (Miller, 1975a). Pregnant females come ashore a few days before birth of their pups which were conceived during the previous breeding season. Parturition occurs from November to January (Stirling, 1971b).

Like other pinniped species of the family Otariidae, female fur seals alternate between foraging trips at sea and regular nursing periods ashore at the natal colony (Gentry & Kooyman, 1986). During the lactation period, pups face periods of rapid nutritional gain followed by fasting periods where weight may be lost (Chilvers *et al*., 1995). This is possible because of an extended period of neonatal dependency and is exhibited by most otariids (Gentry & Kooyman, 1986; Kovacs & Lavigne, 1992). New Zealand fur seal pups are typically weaned at 10-11 months of age (Riedman, 1990). Growth rates of pups can be variable and are influenced by a combination of factors: 1) maternal attendance, 2) milk composition, and 3) pup ingestion ability and suckling behaviour (Gentry & Kooyman, 1986; Lea & Hindell, 1997; Georges & Guinet, 2000).

The initial nursing period after parturition lasts 8-10 days and involves development of recognition between mother and pup (Crawley & Wilson, 1976; Harcourt, 2001). The female will come into oestrus and mate, usually only once and most often around eight days postpartum before departing on a foraging trip (Miller, 1975a; Goldsworthy & Shaughnessy, 1994). Trips last 1-8 days during the breeding season, but increase during the year (McNab & Crawley, 1975; Miller, 1975a; Harcourt *et al*., 1995). At Ohau Point, Kaikoura, on the east coast of the South Island, the duration of foraging trips ranged from overnight to 15 days, with averages of 2-4 days each year (L. Boren, pers. comm.). Mattlin *et al*. (1998) found that cows spent an average of 15 days foraging at sea in October, around weaning time. Periods ashore during which nutritional transfer to the pup occurs last 1-13 days (Miller, 1975a; Harcourt *et al*., 1995; Mattlin *et al*., 1998). Maternal attendance patterns are dependent on food resource availability and environmental conditions (Trillmich, 1990). New Zealand fur seals at Kaikoura have a readily available mesopelagic food source in the Kaikoura Canyon (Carey, 1992) which may explain the short duration of foraging trips.

Mother-pup recognition systems in pinnipeds

The phocid fasting strategy means that females remain near their pup during lactation (Insley, 1992). However in some species females occasionally leave their pup to make short feeding trips and disturbances in dense breeding colonies cause separations, so the existence of a mother-pup recognition system is highly beneficial but possibly not crucial. The short lactation period that characterises phocids may not require a complex recognition system. Lactation length in the hooded seal (*Cystophora cristata*) is only 4 days so females can remain with their pup continuously (Bowen,

1987). The relatively sedentary nature of phocid pups helps mothers to relocate their offspring after brief feeding bouts (Kovacs, 1995).

A number of phocid species have individually stereotyped calls (e.g. northern elephant seal, *Mirounga angustirostris*: Insley, 1992; Hawaiian monk seal, *Monachus schauinslandi*: Job *et al*., 1995; grey seal *Halichoerus grypus*: McCulloch *et al*., 1999; harp seal, *Phoca groenlandica*: Van Opzeeland & Parijs, 2004). Females and pups use vocalisations alongside olfactory, visual and spatial cues to reunite (Kovacs, 1995). However, allosuckling, defined as "care given to a pup in replacement of or in addition to that given by its mother" (McCulloch *et al*., 1999) occurs in several species (e.g. northern elephant seal: Le Boeuf *et al*., 1972; grey seal: Fogden, 1968; Weddell seal: *Leptonychotes weddellii*: Stirling, 1975). Fostering can occur at high levels in phocids, for example up to 90% of female Hawaiian monk seals foster pups, and may be related to density (Riedman & Le Boeuf, 1982; Boness *et al*., 1998). Fostering may indicate a poor recognition system in phocids (McCulloch *et al*., 1999; Insley *et al*., 2003).

A well-developed recognition system is strongly selected for in otariids (Insley, 1992; Phillips & Stirling, 2000; Charrier *et al*., 2003a). Possibly as a consequence of strong recognition, fostering occurs less frequently in otariids than in phocids (Trillmich, 1981; Lunn, 1992; Childerhouse & Gales, 2001). The maternal foraging cycle of otariids means that females leave their pups regularly and for sometimes long periods, so need the ability to find and recognise their pup when they return (Riedman, 1990). The extended period of lactation in otariids requires a longer temporal memory of vocal and olfactory signatures. In some species mother and pup are able to recognise

each other for up to 4 years (Insley, 2000). Long lactation also means a great amount of time and energy resources are invested in pups, so females discriminating among pups and exclusively provisioning their offspring prevents misdirected parental effort that reduces reproductive success (Trivers, 1972).

Reproduction incurs significant costs to females in terms of reduced survival and future fecundity due to reduced pregnancy rate (Boyd, 1995). A great amount of energy is invested in acquiring and processing the nutrients for milk production in addition to that required for the female's own metabolic needs (Clutton-Brock, 1989; Kovacs & Lavigne, 1992). The large body size and advanced state of development at weaning suggests a greater investment in offspring in otariids compared with phocids (Kovacs & Lavigne, 1992). Provisioning milk to non-filial young reduces the amount provided to filial offspring and may increase forage efforts (Clutton-Brock, 1989). This increases the level of maternal investment could result in a decreased ability to produce other offspring (Trivers, 1972).

Pup strategy during maternal absence

Female California sea lions (*Zalophus californianus*) were found to spend longer periods at sea during an El Niño-Southern Oscillation year and the following year due to reduced prey availability (Ono *et al*., 1987). Supplementary feeding of Antarctic fur seal (*Arctocephalus gazella*) pups resulted in females reducing their foraging trip duration, which also suggests that females have the capacity to adjust their time budgets according to environmental variability (Arnould *et al*., 2001). When food availability was low, females maintain offspring growth rate by increasing foraging duration and subsequently decreasing time ashore nursing offspring (Arnould *et al*.,

2001). With shorter periods of female attendance and therefore less milk provisioned, pups grow slower and pup mortality increases (Ono *et al*., 1987; Lea & Hindell, 1997). Nutritionally stressed pups will attempt to steal milk in order to increase their body condition and chance of survival (Bonner, 1984).

Pups should attempt to as much gain nutritional resources as possible to ensure survival (Porter & Trites, 2004). They will often attempt to gain nutrition from females other than their mothers if the benefits of the attempt outweigh the risk of serious injury from the female (Doidge *et al*., 1984). Therefore, starving pups are highly likely to attempt to steal milk in order to survive (Lunn, 1992). In addition to an increased chance of survival, there is a possible size advantage that could result in greater reproductive success as an adult (Bonner, 1984). The advantage of size and condition in the male is significant in highly polygynous seals, including New Zealand fur seals (Bonner, 1984). Male elephant seals, one of the most polygynous species, have been observed to be most persistent and successful at milk stealing (Reiter, 1978).

A pup gains resources by milk stealing or being fostered which could be in addition to those from its own mother (Porter & Trites, 2004). This is beneficial for the pup to ensure a good body condition and a high chance of survival. Therefore pups should be less discriminating when approaching females, as compared to females seeking their pup (Insley, 2001). This demonstrates a parent-offspring conflict, because for the female, the feeding of a non-filial pup is highly selected against due to the reduction of reproductive success and chance of survival for the female and filial pup (Trivers, 1974; Insley, 2001; Roulin, 2002). As pups become more nutritionally stressed, the

benefits of additional nutrition are likely to outweigh costs of approaching unrelated females, and they may become less discriminating to females and possibly alter their vocal behaviour (Charrier *et al*., 2002a). These modifications in begging strategies may represent attempts to gain allomaternal care.

Objectives

The aim of this study was to investigate the process of mother-pup recognition and pup strategies for gaining nutrition in the New Zealand fur seal, *Arctocephalus forsteri*. The development of recognition between mother and pup after birth is an important step in the ability to locate one another throughout lactation so I investigated this and the reunion process (Chapter 2). Pup vocalisations are an important part of the mother-pup recognition system and I investigated both inter- and intra-individual variation and if variation in pup vocalisations was related to the nutritional state of pups (Chapter 3). Milk stealing by pups as an indication of nutritional stress was investigated (Chapter 4). The occurrence of fostering was examined, as well as possible costs to females and pups and potential explanations for this behaviour. The major findings of this study are discussed collectively along with suggestions for future research in Chapter 5.

This thesis presents evidence that mother-pup recognition is an important ability that allows efficient reunions but prevents a high frequency of misdirected parental care. This information gives greater understanding of the biology of New Zealand fur seals and adds profundity to mother-pup recognition and allosuckling studies in other pinniped species.

Chapter 2: Mother-Pup Recognition Behaviour in the New Zealand Fur Seal *Arctocephalus forsteri*

Abstract

In the New Zealand fur seal (*Arctocephalus forsteri*), mothers must discriminate their own pup from numerous others in order to invest in their own offspring and prevent misdirected parental care. Pups must also be able to recognise their mother to allow efficient reunion and decrease the chance of starvation. At the breeding colony at Ohau Point, Kaikoura, New Zealand, I investigated mother-pup recognition using behavioural observations. Mothers and pups engaged in vocal and olfactory interactions soon after birth, and decreased the use of these over time, suggesting their importance in developing and maintaining mutual recognition. Pups played an active role in reunions, and were more active than females because the costs of failed reunion are greater for pups than for females. Pups spent time searching for mothers, approaching and responding to unrelated females but did not alter their searching behaviour during maternal absence. Females were observed with non-filial pups on a few occasions, which appeared to be caused by disturbance, high mother-pup densities and female aggression; however females did not nurse any of these non-filial pups. These results suggest that a well-developed mutual recognition system exists in *A. forsteri*; however disturbance may impair the mother-pup bond and lead to errors in recognition.

Introduction

Mother-offspring recognition is widespread among fur seals and sea lions (Pinnipedia: Otariidae) (Trillmich, 1981; Gisiner & Schusterman, 1991; Fernandez-Juricic *et al.*, 1999; Insley, 2001; Charrier *et al.*, 2002b; Page *et al.*, 2002; Charrier *et al.*, 2003a; Phillips, 2003). Recognition behaviours facilitate reunion following maternal absence for foraging purposes or within colony separations between mother and pup (Phillips, 2003, Insley, 2001). There have been many anecdotal descriptions of reunion behaviour in otariids (Bartholomew, 1959; Stirling, 1970; Marlow, 1975; McNab & Crawley, 1975; Trillmich, 1981). However, there are few quantitative accounts of mother-pup reunion behaviour (Gisiner & Schusterman, 1991; Insley, 2001; Dobson & Jouventin, 2003; Phillips, 2003).

Otariids breed in large dense colonies and exhibit a maternal strategy whereby females alternate periods of foraging at sea with periods ashore during which they nurse pups (Bonner, 1984; Gentry & Kooyman, 1986). On return from foraging, mothers must find their pups in sometimes extremely dense colonies of hundreds of individuals (Boness *et al.*, 1992). Within-colony separations can also occur because of aggression between adults, environmental conditions such as storms (Boness, 1992), pups leaving to play, or females making thermoregulatory movements (Insley, 2001; Dobson & Jouventin, 2003; Phillips, 2003). These frequent separations over an extended lactation period have selected for the development of reliable recognition mechanisms that otariid mothers and offspring utilise to reunite (Insley *et al.*, 2003). A combination of acoustic and olfactory cues are used, with spatial and visual cues assisting in localising individuals (Phillips, 2003; Insley *et al.*, 2003). Acoustic cues

are the initial mechanism, which need to be effective over long distances in a noisy environment (Charrier *et al.*, 2003a). Olfactory cues are used at close range by way of naso-nasal contact before acceptance or rejection of the female or pup occurs (Phillips, 2003).

Mother-pup recognition is developed soon after birth (Charrier *et al.*, 2003b; Mathevon *et al.*, 2004). Pups are able to discriminate their mother's voice a few days after birth but females may develop this ability earlier, probably a few hours after parturition (Charrier *et al.*, 2003b). Mothers and pups engage in calling and sniffing bouts which appear to function in developing recognition (Miller, 1971; Stirling, 1971b; McNab & Crawley, 1975). Both mothers and pups must be able to recognise each other before the mother leaves for her first foraging trip, around 8 days postpartum in the New Zealand fur seal, *Arctocephalus forsteri* (Miller, 1975a). Subantarctic fur seal (*A. tropicalis*) pups respond specifically to playbacks of their mother's vocalisations when they are 2-5 days old, and a female's date of departure depends on her pup's ability to recognise her calls (Charrier *et al.*, 2001a). Galápagos fur seal (*A. galapagoensis*) and Galápagos sea lion (*Zalophus californianus wollebaeki*) pups discriminate the calls of their mothers by 10 days of age (Trillmich, 1981).

Mother-pup recognition behaviours may persist for long periods. Recognition needs to be maintained throughout the lactation period, which is 10-12 months in *A. forsteri* (Stirling, 1971a; Riedman, 1990; Mathevon *et al.*, 2004). Surprisingly, northern fur seal (*Callorhinus ursinus*) mother-pup pairs have been shown to recognise each other three years after the cessation of lactation, which might suggest that such recognition

behaviours could be useful in a broader context, perhaps as part of a kin recognition process that influences the social structure of seal colonies (Insley, 2000).

Reunion is crucial for survival of pups and prevention of misdirected parental care that may unnecessarily increase energy expenditure and reduce reproductive success of females (Riedman, 1982). Fostering and pup mortality due to mother-pup separation appear to be higher in phocid species such as in the northern elephant seal, *Mirounga angustirostris*, where recognition appears to be generally less developed than in otariids (Riedman & Le Boeuf, 1982; Insley *et al.*, 2003). Natural selection should favour parents that provide resources only to their genetic offspring in order to maximise parental fitness (Beecher, 1991). Therefore, selection favours females that discriminate filial pups from non-filial pups (Phillips & Stirling, 2000). Failures in recognition may result in fostering, which incurs costs of expenditure of additional energy and a decrease in reproductive success if genetic offspring do not survive due to lack of sufficient nutrition (Phillips & Stirling, 2000; Charrier *et al.*, 2003a).

The greater costs to pups (than to mothers) of failed recognition are likely to result in different selective pressures and therefore different behaviours between mother and pup during searching (Insley, 2001; Insley *et al.*, 2003). Pups should be less discriminating toward females than females should be toward pups (Insley, 2001). However, in approaching strange females, a pup runs the risk of being injured, but the risk of starvation is an even greater cost to pups. Insley (2001) found that pups made more calls and travelled further than females during reunions after a maternal foraging trip, suggesting that pups expend more energy in their attempts to reunite than mothers.

Pups may alter their female-searching behaviour under nutritional stress during maternal absence (Charrier *et al.*, 2002a). Females may also alter their behaviour in response to environmental fluctuations. For example, Soto *et al.* (2004) observed female South American sea lions aggressively abducting non-filial pups, accounting for 2.5-8.4% of total pup mortality in the year after a peak of El Niño.

This study on the New Zealand fur seal, *Arctocephalus forsteri*, quantifies the postpartum utilisation of mother-pup vocal and olfactory communication that is important in the development of mutual mother-pup recognition. Mother-pup searching and reunion behaviours are quantified and incidences of possible recognition errors are described. The possible behavioural implications of maternal absence on the searching behaviours of pups are also investigated, as nutritional stress is expected to result in different behaviours.

Methods

Study site

Field work was carried out at Ohau Point seal colony, 26 km north of Kaikoura (42°3S/173°4E) on the east coast of the South Island, New Zealand (Figure 1). Field work was undertaken during two austral summers from November 2003-April 2004 and November 2004-January 2005. For ease of presentation the 2003/4 and 2004/5 seasons will hereafter be referred to as 2003 and 2004, respectively.

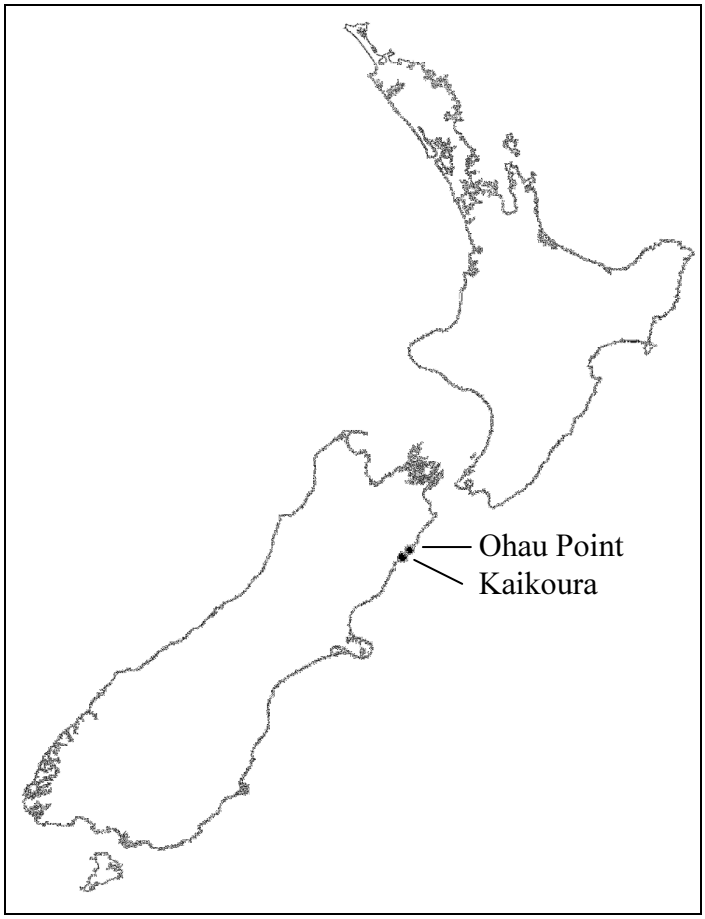


Figure 1. New Zealand map showing the location of Ohau Point seal colony north of Kaikoura, South Island.

Ohau Point seal colony is a boulder outfall at the base of a cliff and contains numerous caves and crevices (Figure 2). Tide pools and rock islands were numerous. It extends 500 metres from the Ohau Point Seal Colony car park north to Ohau Stream and is 30-40 m wide in most areas. The colony was divided into eight sectors but behavioural data were collected in only five areas. Observing seals in other areas posed numerous difficulties (large boulders meant many seals were out of view) and were not persisted with further. Behavioural observations were made from the roadside or from further down the slope at distances of 10-40 metres from the edge of the colony. Identifying seals and observing behaviour was aided with Olympus 8 x 40 binoculars and a spotting scope (20-60x magnification).

Figure 2. Rocky terrain of Ohau Point seal colony.

Animal identification

In 2003, 170 pups were marked with a unique combination of haircuts, numbered caps glued to their fur, and flipper tags (Allflex sheep tags, Allflex New Zealand Ltd, Palmerston North). A total of 75 adult females were identifiable from tags (new and old) and natural markings. VHF radio telemetry transmitters (Sirtrack Ltd, Havelock

North, NZ) were attached to 19 adult females to identify periods of maternal absence from January to March 2004. These females were either flipper-tagged or had numbered caps glued to their fur. An omni-directional antenna (Sirtrack Ltd, Havelock North, NZ), R2100 receiver and D5041 data logger (Advanced Telemetry Systems Inc., MN, USA) were left at the centre of the colony, allowing signals to be picked up throughout the colony at 30 minute intervals.

In 2004, 62 pups were marked, 12 females were tagged and around 120 females were individually identifiable. VHF radio telemetry transmitters were attached to 14 females and presence/absence data collected at 15 minute intervals in January 2005. The number of marked pups was reduced from the previous season because there were fewer projects running requiring marked pups and consequently fewer fieldworkers and resources were available for this research in 2004.

Behavioural observations

Three different sets of data were collected: on mother-pup interactions after birth to investigate the development of recognition, on female-initiated reunion attempts, and pup searching behaviour to investigate mother-pup recognition and the reunion process from the females' and pups' perspectives, respectively. All behavioural data was collected using focal animal sampling (Altmann, 1973).

Mother-pup interactions

Observations of births and mother-pup interactions were conducted using focal animal sampling from 29 November 2003 – 11 January 2004 (pups were 0 – 25 days old) and 23 November 2004 – 15 December 2005 (pups were 0 – 5 days old). There were

fewer observations in the second season because time was more limited. Where births were not observed, fresh blood or the presence of a placenta (which were usually taken by gulls soon after birth) next to a mother-pup pair evidenced a recent birth that day (L. Boren, pers. comm.; pers. obs.). Pups were wet, unsteady and uncoordinated soon after birth. A white/pink or bloody umbilicus also indicated a birth that day. Webbing between the toes was pink up to a few days after birth. Umbilical cords became blackened and dried up a few days postpartum, and pups without umbilical cords were estimated to be at least three days old. Pups were able to be followed on further days by their location (only at the start of the season when there were few pups, as they did not usually move in the first few days postpartum) or if the mother was identifiable by natural markings or old tags. Pups were marked before the pair moved to a new spot in the colony.

Focal observations lasted from thirty minutes to three hours in duration, however some ended prematurely when mother-pup pairs separated or moved out of sight so these were not used in analysis. Pairs were defined to be together when they were less than one metre apart. Any time apart was excluded from analysis. When together, the length of time mothers and pups each spent resting (not visually aware of surroundings), active/alert (included moving around within one metre of each other, grooming, comfort movements, sitting or lying down alert) and nursing was recorded.

Pup-attraction calls emitted by the mother and female-attraction calls emitted by the pup were recorded during all observation bouts. Calls that were obviously not pup or female-attraction calls, such as growls when a pup bit his mother or screams when a pup was being picked up by his mother, were not included. The frequency of olfactory

contacts were recorded in two forms: where the mother and pup made naso-nasal contact, which involved the sniffing and light contact between their noses, with vibrissae held erect; and where the mother sniffed the pup on any other part of the pup's body apart from the nose (usually on the pup's back or the top of the head), also with vibrissae erect (Miller, 1975b). Mouthing behaviour by the female was also documented, where she would open her mouth and place it on the pup, usually on the pup's head or face but sometimes the back, as if she was lightly biting it (Miller, 1974). The rate of female calling, pup calling and olfactory contact (both types) were calculated from the time the pup and the female spent active/alert, as mothers and pups did not interact when one or both were resting or the pup was nursing. Female active time was used to calculate the rate of olfactory contact per minute because olfactory contacts were most often initiated by the female (pers. obs.).

Female-initiated reunion behaviour

Observations of female-initiated reunion attempts and reunions (from here on attempts and successful reunions are both referred to as "reunions") using focal-animal sampling were made between 20 December 2003 – 7 March 2004 and 14 December – 19 January 2005. Two reunion types were documented: when mothers returned to the colony from the sea ("offshore" reunions), or had been in the colony and separated from their pup ("onshore"). Only onshore reunions where the mother and pup were more than five metres apart were included for analysis.

Focal observations began when a female began making pup-attraction calls, accompanied by searching head movements. The distance travelled by the female while searching was estimated to the nearest metre, with the aid of measured paint

marks made earlier in the season on rocks in the observation areas. The frequency of pup-attraction calls emitted by the searching female was recorded. I recorded the behaviour of pups that responded vocally to the calling female (by vocalising immediately after a pup-attraction call), that approached the female, or were approached by the female, to within two metres, but without making contact, and pups that made contact with the female.

Reactions of approached (or approaching) females to non-filial pups were also documented. These ranged from open mouth threats, huffs and growls, through to lunges and chases. For open-mouth threats a female opened her mouth, with no vocalising, at the pup. A lunge was defined when a female quickly darted her head toward a pup with her mouth open, as if she was about to bite. A chase involved a female moving her whole body toward a pup and pursuing the fleeing pup for a short distance. A huff was when a female blew an audible puff of air through an open mouth at the pup. A growl was a deep vocalisation directed at a pup. In many cases it was not known if a pup was non-filial or filial until contact was made and the pup was either ignored, rejected or accepted (as many focal animals were unidentifiable), so vocalisations and distances travelled by all responding pups were documented. After it was discovered who the filial pup was, the distance travelled and calls emitted by the searching female from when her pup began responding was calculated. Search observations ended at the reunion point if it was successful, which was defined as such when no antagonistic behaviour was evident after naso-nasal investigation. If the female made no further pup-attraction calls after ten minutes, the search was considered unsuccessful at the point of the last call. Focal observations on successful reunions ended five minutes after the reunion point or at the commencement of

nursing if it occurred before five minutes had passed. The behaviour of mother and pup were recorded between the reunion point and the end of observation, including frequencies of calls and olfactory contacts. If a focal female went out of sight and did not reappear, observations ceased and these were not used in the analysis.

Pup searching behaviour

Focal animal observations were carried out on marked calling and searching pups from 5 - 28 January 2005 (14 days of observations). A search began when a pup began calling, either in response to a female or spontaneously, and making searching head movements. Searches ended at the point of the last call, when no further calling was observed for ten minutes. I recorded the distance travelled, number of female-attraction calls emitted, number of approaches within two metres of unrelated females, and number of contacts with unrelated females (either by naso-nasal contact or the female sniffed the pup). It was noted whether a pup began calling in response to his mother (if known), another female or if it began calling spontaneously. The search was deemed successful if the pup made contact with a female and was accepted (not rejected with threats).

Statistical analysis

Minitab 14 and SPSS 11.5 were used for statistical analyses. Spearman's rank correlations (Dytham, 1999) were undertaken to test for an association between pup calls, mother calls and olfactory contacts and pup age during mother-pup interactions. The median pupping dates were used (5 December in 2003; 7 December in 2004) to estimate pup age. A Wilcoxon signed-ranks test (Dytham, 1999) was used to compare reunion effort between mothers and pups in terms of distance and vocalisations.

Kruskal-Wallis tests (Dytham, 1999) were carried out to test the difference in four variables for each year (search duration, number of calls, call rate and distance travelled) between the four reunion types. Spearman's rank correlations were undertaken to examine changes in search duration, number of female calls, female call rate and female distance travelled, with pup age. Median pupping date was again used to estimate pup age since the majority of reunions involved unidentifiable animals and when reunions involving unidentifiable females were unsuccessful, the filial pup was of course unknown. Pup searching data were analysed using Spearman's rank correlations to find association between search variables (number of searches, % time spent searching, distance, number of calls, number of females approached, number of females contacted) and pup age (taken as days since the median pupping date of 7 December). Mann-Whitney tests were used to find differences in pup searches between those pups whose mothers were present and those who were absent. Spearman's rank correlations tested for association between search variables and the number of days the mother had been absent from the colony. However, for these tests, only seven pups whose mothers were reliably identifiable were used. Kruskal-Wallis tests were used to test for individuality of pups within each search variable.

Results

Recognition ontogeny

Only four births were witnessed over both seasons. Females began sniffing and mouthing the pup immediately after birth. Mouthing appeared in some cases to assist removal of the placenta from the pup's head and face, however mouthing was observed frequently a few hours after birth, and for one mother-pup pair, up to one day postpartum. Naso-nasal contacts initiated by the female also occurred (Figure 3). Females frequently picked pups up in their mouths, presumably to try to keep them close. One female was observed intentionally lying on top of her newborn, even rising to readjust the pup and lying back down. Pups began calling between two and 13 minutes postpartum. Females began making pup-attraction calls from two to over 30 minutes postpartum. Some mother-pup calling bouts (where they would call back and forth to each other) occurred but pup calls were mostly spontaneous. Pups would nearly always reply to pup-attraction calls emitted by their mother.

Female call rate decreased with pup age (r_s = -0.325, n = 65, P= 0.008; Figure 4), as did pup call rate (r_s = -0.396, n = 68, P= 0.001; Figure 5). Female call rate also increased with pup call rate (r_s = 0.393, n = 65, P= 0.001). Pups vocalised, on average, at 14 times the rate of their mothers. The rate of olfactory contact, through both mothers sniffing pups and naso-nasal contact between mother and pup, decreased with pup age (r_s = -0.612, n = 67, P< 0.001; Figure 6).

Figure 3. Naso-nasal contact between mother (with radio transmitter) and pup.

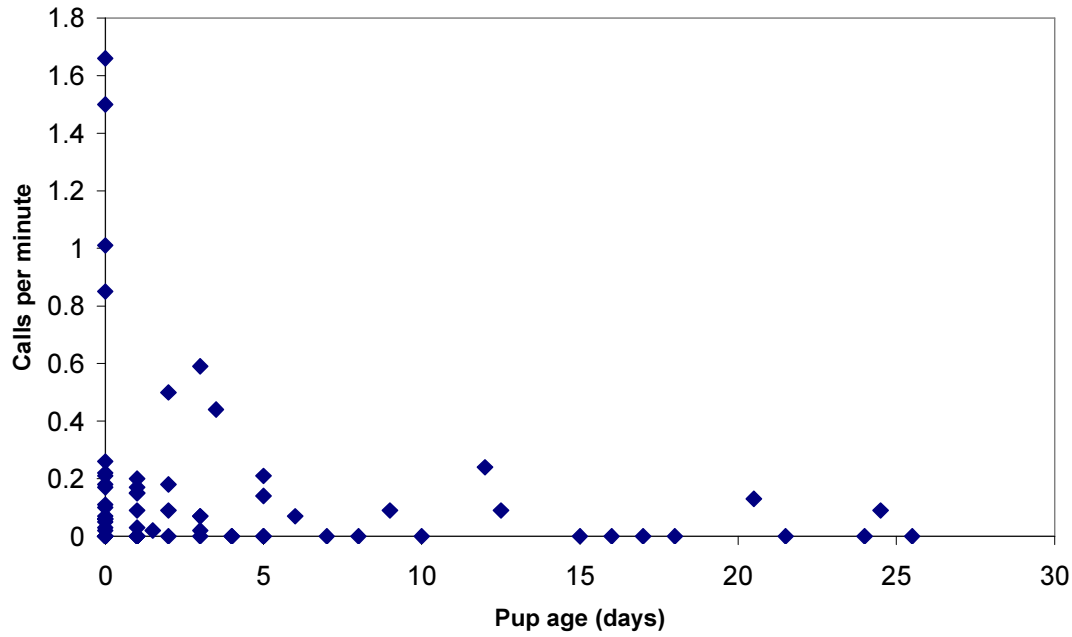


Figure 4. The relationship between the rate of female calls (pup attraction calls) and pup age in days during mother-pup interactions. Each point represents the calling rate for each focal observation.

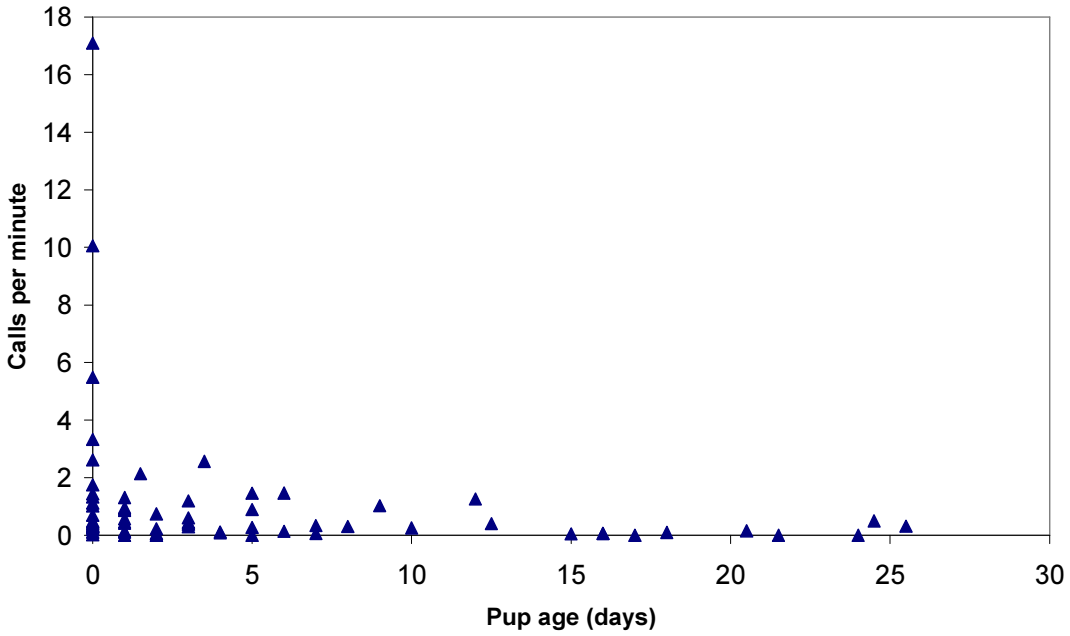


Figure 5. The relationship between the rate of pup calls (female attraction calls) and pup age in days during mother-pup interactions. Each point represents the calling rate for each focal observation. Note the difference in scale from Figure 4.

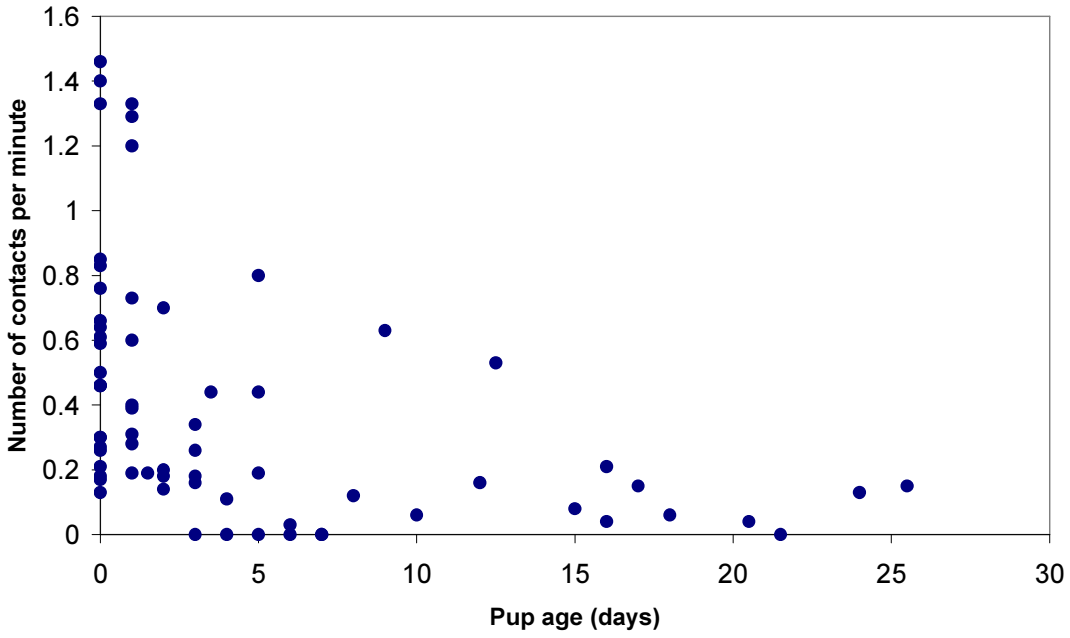


Figure 6. The relationship between the rate of olfactory contacts (mother sniff pup and naso-nasal contact between mother and pup) and pup age in days during mother-pup interactions. Each point represents the calling rate for each focal observation.

Female-initiated reunion behaviour

There was a significant difference among the frequencies of the four different reunion types (onshore and offshore vs. successful and unsuccessful; Table 1) for both years ($\chi^2 = 7.37$, df = 1, P=0.014). Of the 150 initial reunions observed, 47.3% were successful. Offshore reunions (those after females returned from the sea) were more successful than onshore reunions (those following onshore separation). The shortest reunion attempts lasted only a few seconds (for example, when females made only one call) and usually occurred during an onshore reunion after a female had been resting. The longest reunion took 77 minutes, with the average being 10.2 minutes.

Table 1. Frequencies of the four reunion types observed in both years, in terms of whether they were offshore reunions, after females returned from the sea, or onshore reunions, after onshore separation, and whether they were successful or not.

	Successful	Unsuccessful	**Total**
Onshore	23	43	**66**
Offshore	48	36	**84**
Total	**71**	**79**	**150**

In 2003, there was a significant difference in the number of female calls between the four reunion types (Table 2). There were a greater median number of calls during offshore reunions than onshore reunions. During onshore reunions, there were a greater median number of calls during successful reunions than unsuccessful reunions. However, there were no significant differences in search duration, call rate and distance travelled between the reunion types (Table 2). In 2004, search duration, the number of female calls, call rate and distance travelled did not differ significantly between different types of reunion (Table 2).

Table 2. Differences in female behaviour during the four reunion types: duration of search, number of calls emitted, calls per minute and distance travelled. Values are expressed as medians. Sample sizes are listed in the row specifying the year for each category and where there are exceptions they are in brackets. Test statistics (*H*) and *P*-values stated from Kruskal-Wallis tests (df = 3).

	Offshore success	Offshore unsuccessful	Onshore success	Onshore unsuccessful	*H*	*P*
2003	N = 28	N = 21	N = 11	N = 27		
Search duration (min)	5.0	12.0	6.5	2.0	5.12	0.163
Number of calls	11.5	11.0	9.0	3.0	13.02	**0.005**
Calls per minute	1.80	1.00	1.89	1.00	6.75	0.080
Distance (m)	6.0	7.0	7.0	1.5	6.14	0.105
2004	N = 20	N = 15	N = 12	N = 16		
Search duration (min)	4.5	15.5	7.1	2.6	6.71	0.082
Number of calls	6.0 (19)	9.0	12.5	3.5	6.84	0.077
Calls per minute	1.71 (19)	1.02	1.39	1.38	1.63	0.652
Distance (m)	5.0	5.0	5.0	0	5.10	0.165

All successful reunions (where reunion behaviour was clearly visible as some occurred out of sight, for example behind a rock) (n = 78), except one involved olfactory contact (Figure 7). In this case, the responding pup approached his mother in the same spot they were last observed together. The female then simply exposed her belly and allowed him to nurse without olfactory confirmation. Here the female seemed to recognise the pup solely on vocal identity. Since the mother did not call, the pup could not have known the identity of the female but may have used the location as a clue. Other searching pups were observed approaching the exposed bellies of unrelated females in the same location they were frequently observed with their mother. Females presumably would not be able to identify her pup solely on his vocalisations if there were other pups calling at the same time. These pup-initiated reunions were observed more frequently later in the breeding season. Visual cues may have been involved in reunion attempts in addition to vocal and olfactory cues, as wet females appeared to be attractive to pups and even wet sub-adult males emerging from the sea were occasionally approached by pups.

a

b

c d

Figure 7. Female-initiated reunion behaviours a) female making pup-attraction call b) non-filial pups approaching searching female c) successful reunion: naso-nasal contact d) successful reunion: naso-body contact.

At the time of reunion and the period immediately after (up to 5 minutes post reunion or until nursing took place), 0 - 14 (average 2.8) naso-nasal contacts occurred and the mother sniffed the pup 0 – 14 times (average 1.6). At or immediately after reunion, pups vocalised in 68% of observations, whereas mothers vocalised in 22% of observations. Pups often became excited on reunion, made short and loud calls, shook their bodies, and pushed their heads into the mother's neck or head. Successful reunion was followed by nursing in 62% of observations (n=66). In 24% of successful reunions, both the female and pup remained active or alert (including interacting, sitting, grooming, moving or lying alert), whilst in 8% of observations mother and pup separated again (over one metre apart) within 5 minutes. In the minority of occasions, mother and pup both rested (4%), while in 2% of observations the female rested while the pup remained active or alert.

One to seven non-filial pups vocalised in reply to pup-attraction calls emitted by females during 51% of reunions. One to two non-filial pups also approached the searching female or were approached by the female in 20% of reunions (Figure 7), with females making contact with between one and four non-filial pups during 29% of reunions. Females reacted in a number of ways to approaching pups or to pups after olfactory contact (n=113 pups): 46% open-mouth threat, 33% no reaction, 8.8% growl, 7.1% bite, 2.6% huff, 1.7% lunge and 0.8% chase. Pups occasionally reacted first with an open-mouth threat immediately after contact before the female could react.

Filial pups travelled further during successful reunions than their mothers during all parts of the season, but this difference was not significant (Table 3). Pups made significantly more calls during reunions than their mothers (Table 3).

Table 3. Mother and offspring reunion behaviour during successful reunions: distance travelled (n=40) and the number of calls emitted (n=39). Values expressed as medians. Wilcoxon signed-ranks test statistic (*Z*).

Variable	Mothers	Offspring	*Z*	*P*
Distance travelled (m)	0.75	4.00	-1.90	0.058
Number of calls during reunions	4.00	5.00	-2.90	**0.004**

In 2003, search duration of mothers declined as pups got older (r_s=-0.221, n=88, P=0.038; Figure 8). As pup age increased, neither female call rate (r_s=-0.076, n=88, P=0.484), distance (r_s=-0.010, n=87, P=0.925) nor the number of calls (offshore reunions: r_s=-0.193, n=49, P=0.183; onshore reunions: r_s=-0.238, n=39, P=0.145) decreased significantly. In 2004, females emitted fewer calls during reunions as pups became older (r_s=-0.347, n= 62, P=0.006; Figure 9). The distance that females travelled also decreased with increasing pup age (r_s=-0.311, n=59, P=0.016; Figure 10). However, the distance that filial pups travelled during successful reunions significantly increased with pup age (r_s=0.487, n=40, P=0.001; Figure 11). Search duration (r_s=-0.203, n=63, P=0.110) and rate of calling (r_s=-0.149, n= 62, P=0.246) did not significantly change with increasing pup age. In both years, females travelled greater distances as search duration increased (2003: r_s=0.408, n=87, P<0.001; 2004: r_s=0.301, n=59, P=0.020). Females appeared to weary of calling as call rate decreased with increasing duration of searches (2003: r_s=-0.398, n=88, P<0.001; 2004: r_s=-0.510, n=62, P<0.001). In 2004 only, the absolute number of female calls

increased with search duration (r_s =0.707, n=62, P<0.001) and the distance travelled increased with the number of female calls (r_s =0.480, n=58, P<0.001).

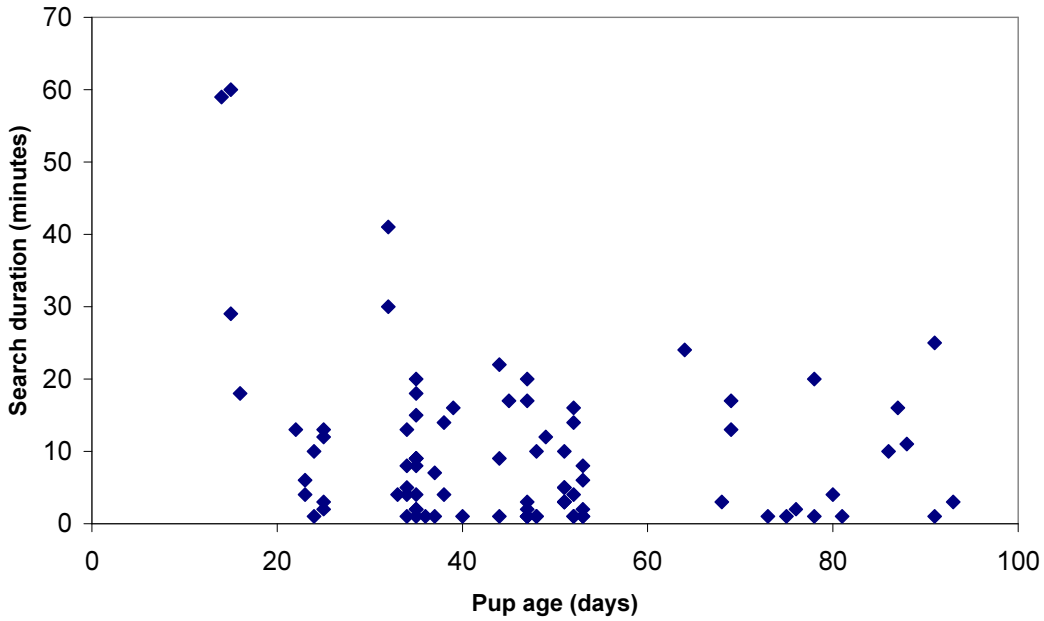


Figure 8. The relationship between female search duration and pup age in days (from median pupping date) during female-initiated reunions. Each point represents a search by a female. Data for 2003 only.

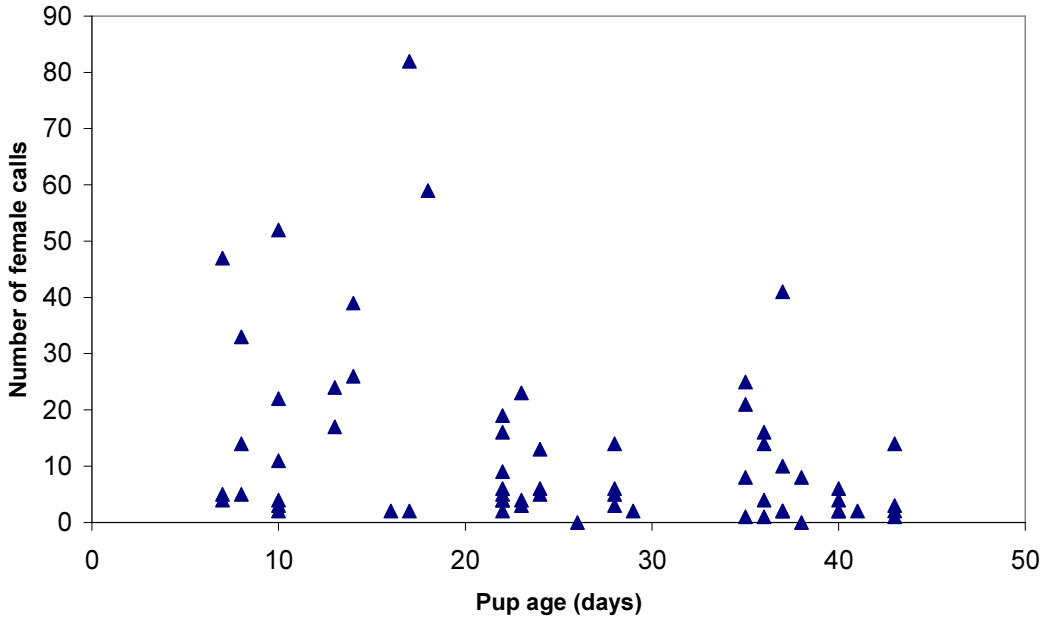


Figure 9. The relationship between the number of female calls (pup-attraction calls) and pup age in days (from median pupping date) during female-initiated reunions. Each point represents a search by a female. Data for 2004 only.

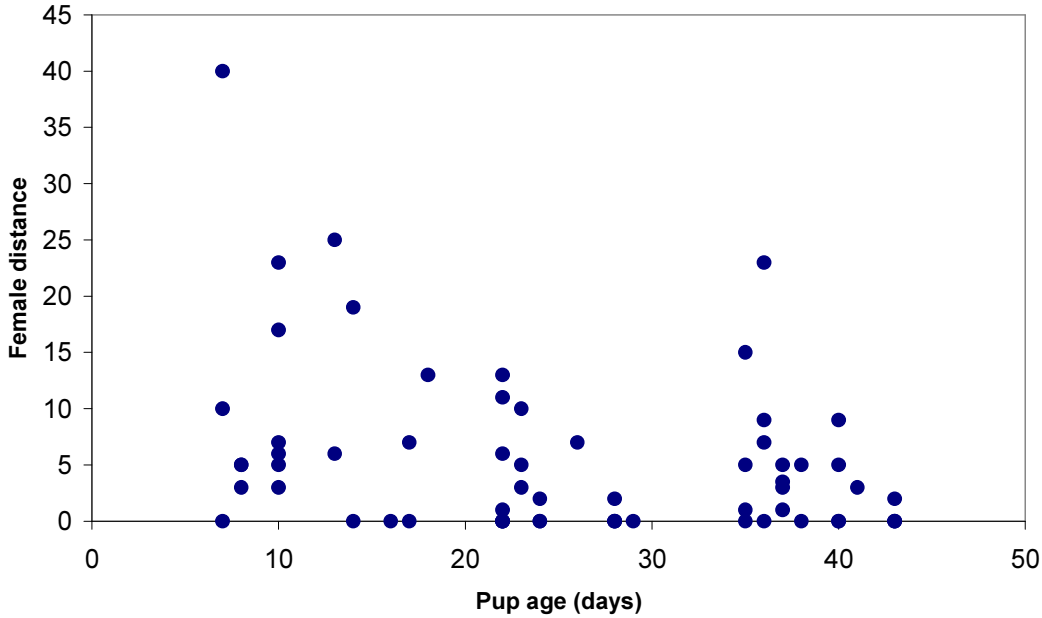


Figure 10. The relationship between the distance travelled by females and pup age in days (from median pupping date) during female-initiated reunions. Each point represents a search by a female. Data for 2004 only.

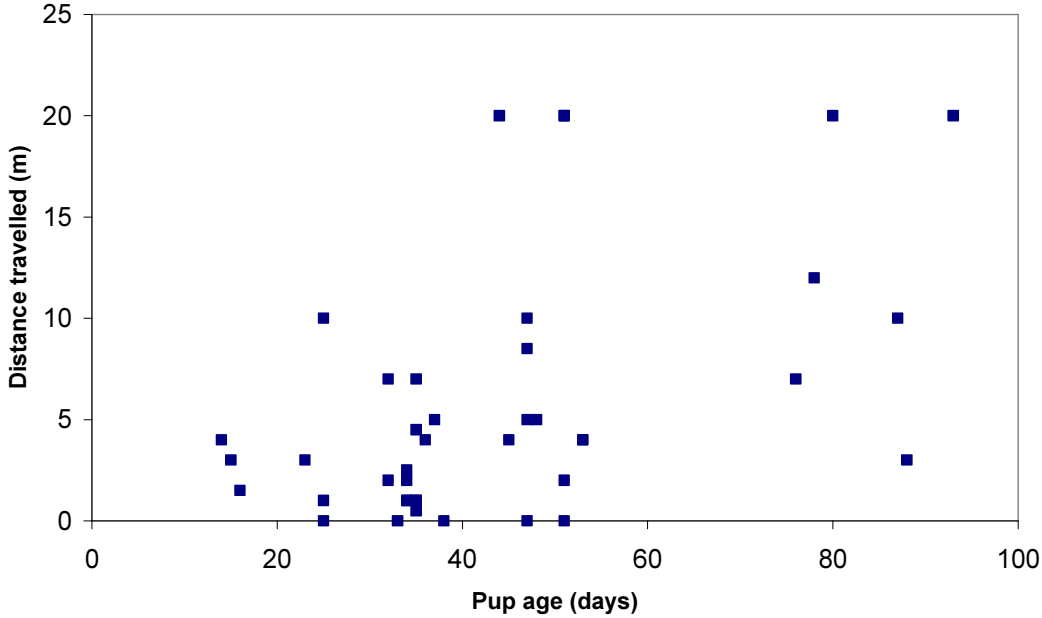


Figure 11. The relationship between the distance travelled by the filial pup and pup age in days (from median pupping date) during successful female-initiated reunions. Each point represents a search by a pup during a female-initiated reunion. Data for 2003 only.

Pup searching behaviour

Pup searches ranged from a few seconds, when only one call was made, usually in response to a female, to 25 minutes (the endpoint of a search was at the last call emitted, when no further calls were made during ten minutes). The average search time was only 1.9 minutes. Pups made 0-6 searches per day. Of 369 pup searches, 18% were successful and of these successful searches, the pup had been observed with his mother previously that day 42% of the time. The low success rate is most likely because some searches took place while mothers were not present in the colony. Thirty-nine percent of pup searches began when the pup vocalised in response to a calling female, but the majority of searches began with spontaneous calling. In 11% of searches, pups made only one vocalisation in response to a female and did not move toward the calling female. Pups approached but did not contact unrelated females (1–7 females) in 13% of searches and contacted unrelated females in 13% of searches (1–6 females).

There was no association between any of the search variables measured and pup age (number of searches: r_s=0.107, P=0.075, n=279; % time searching: r_s=-0.017, P=0.817, number of calls: r_s=0.023, P=0.755; distance travelled: r_s=0.023, P=0.757; number of females approached: r_s,=-0.102, p=0.168; number of females contacted; r_s=-0.035, P=0.637; sample sizes unless specified are n=183). However, many variables co-varied, for example, the more time pups spent searching, the greater the distance travelled (r_s=0.583, P<0.001, n=183) and the greater number of calls emitted (r_s=0.620, P<0.001, n=183). The greater the distance pups travelled, the more calls emitted (r_s=0.829, P<0.001, n=183), the greater number of females approached (r_s=0.279, P<0.001, n=183), and contacted (r_s=0.289, P<0.001, n=183).

There was no significant difference between the number of searches made by pups when their mother was present in the colony and when she was absent (Table 4). Pups made a significantly greater number of calls during searches when their mother was present (Table 4). Pups travelled further when their mother was present than when she was absent but this difference was not significant (Table 4). There was also no significant difference in the proportion of time spent searching between searches when mothers were absent and those when mothers were present (Table 4).

Pups did not significantly alter their search effort over time during maternal absence, which was one to four days after the mother left the colony (number of searches: r_s=-0.265, P=0.273; proportion of time searching: r_s=0.444, P=0.057; calls emitted: r_s=0.004, P=0.987; distance travelled: r_s=0.011, P=0.965; all sample sizes n=19 searches).

The number of calls, distance travelled and the number of females approached and contacted did not differ among pups (Kruskal-Wallis, df=24: calls: H=21.82, P=0.590; distance: H=23.54, P=0.488; females approached: H=15.39, P=0.909; females contacted: H=19.97, P=0.699). However, the number of searches and the proportion of time spent searching did differ among pups (Kruskal-Wallis, df=24, number of searches: H=38.65, P=0.030; proportion time searching: H=97.06, P<0.001). Therefore, to ensure that analyses were not confounded by differences among pups for the number of searches and proportion of time searching, pups with apparently different values (two pups for the number of searches and six pups for the proportion of time searching) were excluded in a stepwise manner until there was no difference among pups and all tests carried out a second time. This did not result in

any different outcomes, indicating that the search variables themselves were responsible for any significant results rather than pup individuality.

Table 4. Differences in medians of search variables (the number of searches, the proportion of time searching, the number of calls and the distance travelled) between searches by pups when the mother is present (n=36) and when the mother is absent (n=21). Mann-Whitney (*W*) statistics and *P* values are shown.

	Present	Absent	*W*	*P*
Number of searches	2	1	1157.0	0.063
Proportion of time searching	0.02	0.01	1095.5	0.398
Number of calls	15	4	463.0	**0.016**
Distance travelled	9	3	1149.5	0.082

Recognition 'error'

Errors in recognition of pups by females are difficult to quantify as it is often unknown whether or not a female does not recognise a pup or is unmotivated to reject it, perhaps because of a disturbance. A female may also attempt to abduct non-filial pups because she has lost her own, in which case she may gain benefits of maternal experience by nursing a pup (Marlow, 1970; Riedman & Le Boeuf, 1982; Boness *et al*., 1992; Schaeff *et al*., 1999). Despite recognition errors being difficult to conclude as such, they are interesting as in some cases, these behaviours may lead to fostering (Rand, 1955). Below I describe a number of qualitative accounts of interest.

Pup swapping

In December 2004, there was an interesting case where two females fighting over space ended up swapping pups for almost one hour, with one female apparently unaware of the swap and 'abducting' the pup, and the other female attempting to get her pup back (Figure 12). The density of mother-newborn pairs appeared to be greater in this area than in other areas. There were about four pairs in an area of approximately 10 m^2. The pup that was 'abducted' was believed to be two days old and the other pup of similar age. The pups were distinguishable by their size and one female, the mother of the abducted pup (female 1), was identifiable by tag tears in her flippers. Observations began when two nearby mother-newborn pairs were fighting, apparently over space. During their fighting, the abductee pup moved to the side of the unrelated female (female 2). Female 2 made naso-nasal contact with him and made an open-mouth threat to her pup. Over the next five minutes, the abductee pup and female 2 engaged in calling and olfactory contact bouts. Female 1 called to him,

but ignored female 2's pup. Female 2 then picked up the non-filial pup. At one point both the non-filial and her filial pup were nearby female 2, and she made naso-nasal contact with both many times, but ignored her own pup and picked up the non-filial pup. Fifty-three minutes after the swap first took place, female 2 returned to her pup, fully accepting him and the abductee pup ended up back with his mother.

a b c

Figure 12. Case where female confuses pups and "abducts" a non-filial pup
a) females fighting, with their own pups (left female's pup is behind her) b) pup of female on right nuzzles the unrelated female c) female with the non-filial pup to her left; wet female to the left is the mother.

In December 2004, a similar encounter was observed, wherein two females were fighting over a marked female pup five to six days old. A female, presumably the mother, picked up the pup then a few minutes later a second female made naso-nasal contact with the pup and called to her. At this point there was a male-initiated disturbance during which the second female picked the pup up, most likely as a response to remove the pup from the apparent danger of the male. The pup's 'mother' fought with this female but the female repeatedly picked up the pup to bring her closer. The pup even nosed around this female's belly in an attempt to nurse, but after thirteen minutes, the pup's mother managed to chase the second female away and was reunited with her pup.

Female associations with non-filial pups

In December 2003, while we were marking pups in the colony, a known female picked up and dragged off her filial pup that we had just returned to her following temporary marking of the pup. She left this pup and retrieved a non-filial pup that we had returned to the same spot from which the pup was initially caught. She remained with this non-filial pup for ten minutes and was still with him when observations ended. No nursing of the non-filial pup was observed, and no calls or olfactory contacts were observed between the pair. After this occurrence the female was always observed with her filial pup. There was a similar case documented in 2004, again influenced by disturbance, where a female tolerated the presence of a non-filial pup alongside her own pup for about five minutes but she eventually threatened the non-filial pup (Figure 13).

There were five cases of females (two in 2003, three in 2004) not rejecting a non-filial pup when attempting to reunite with their filial pup. All cases occurred at least four weeks after the median pupping date. In every case, two pups approached the female at or around the same time, often with both calling, which probably confused the female. All five non-filial pups began to nuzzle the belly of the female with no rejection for around 10 – 30 seconds. It was not known if these pups managed to obtain milk. In two cases, pups became excited, shaking their bodies while making short and loud calls as some did when reuniting with their mother. They were not rejected until the female made contact with her filial pup. Pup behaviour here was different to the milk stealing behaviour described in Chapter 4, because these pups vocalised and made olfactory contact with the aware females before nuzzling their belly, whereas during milk stealing attempts pups would silently and directly approach the belly, not the head of the female. Three pups were threatened and the other two left on their own accord after the female made naso-nasal contact with them again.

Figure 13. Identifiable female with filial and non-filial pup. a) Non-filial pup (with haircut) nuzzles the female's chest, the filial pup is to the left. b). Female finally rejects the non-filial pup by biting him.

Discussion

Development of recognition

Olfactory contact through female naso-nasal and naso-body contact occurs immediately after birth. Olfactory communication was observed between mothers and pups in all observations of 0-3 day old pups. In contrast, vocalising between mother and pup appears more variable, commencing two minutes postpartum at the earliest and up to 13 minutes for the pup and longer than 30 minutes for the female. Calling rates for mother-pup pairs in this study varied from 0-1.7 female calls and 0-17 pup calls per minute on the day of birth. Learning each other's vocalisations probably occurs after olfactory recognition, supported by the observation that olfactory contact is the definitive identification in mother-pup reunions.

More frequent calling in pups than females in this study, supported by McNab & Crawley (1975), also on New Zealand fur seals, suggests that rapid vocal recognition is more important for the female than the pup. Frequent calling in pups soon after birth would allow a mother to quickly learn her pup's vocalisations. This is beneficial as although females usually do not depart for the first foraging trip until 8 days postpartum (Miller, 1975a), they often leave their pup to swim for short periods and are required to re-locate and recognise their pup (pers. obs.).

The exact timing of recognition was not determined in this study; however it appears that the timing differs between females, as some females appeared to make mistakes in identifying their pup when they were a few days old. Reiter *et al.* (1981) found that older northern elephant seal females were better at establishing the mother-pup bond,

perhaps because they were more experienced. The ability of pups to recognise their mother probably also varies between individuals but presumably must occur before their mothers' first departure. A subantarctic fur seal pup learns their mother's calls 2-5 days postpartum and their mother adjusts the date of departure accordingly (Charrier *et al.*, 2001a).

Mother and pup calling rates and rates of olfactory contact, when mothers and pups were in association, generally decreased with pup age (Figure 4-6). Pups were not able to be followed throughout development because of the great difficulty in locating them on subsequent days due to the terrain of the colony. Large boulders, crevasses, caves and ridges obscured pups from view. This limits what can be concluded from these observations, as mother-pup pairs appeared to be highly variable in their communicatory behaviours. However, there were general trends, indicating decreasing importance of high rates of communication as recognition became well developed. Maintenance of the recognition bond is necessary, and frequent calling during and immediately after reunions probably suffices vocal recognition. When pups were two weeks old (after the females' first foraging trip), calling rates of mothers and pups while together were near zero. Rates of olfactory contact decreased around the same time, but were still present at levels of around 0.1 contacts per minute.

Playback experiments were beyond the scope of this study but would have been a useful method to learn the exact timing of recognition ontogeny. Playbacks were employed by Charrier *et al*. (2001a) to find the timing of recognition of female calls by subantarctic fur seal pups.

Recognition errors

The cases of non-filial 'pup abduction' where females accepted non-filial pups under human disturbance and females stole or attempted to steal pups under female disturbance all occurred early in the season, suggesting that these females had not yet fully learned to recognise their pups. However in the first cases, the females ultimately reunited with, and fully accepted their filial pups. In the other case the female ended up with the correct pup but this was facilitated by the other female who recognised her pup and managed to steal him back. The mistaken female's pup was at least one day old, suggesting that some females take longer to recognise their pup; however the high density of mother-pup pairs and the distraction caused by female-female aggression probably facilitated this occurrence. Similarly, the case of a female unsuccessfully attempting to steal a female's pup began by female aggression and male disturbance. Females abducting or swapping pups has also been observed under high densities in the Australian sea lion (Marlow, 1972). There were a greater number of pups born in the second season (2003: 291; 2004: 451; L. Boren, pers. comm.), suggesting density may have increased, and the only cases of females fighting over pups were observed in this season. Different environmental conditions in the second season with El Niño southern oscillation may also have been a factor, as supported by the finding of female Southern sea lions exhibiting aberrant behaviours such as abducting and killing newborn pups during the extreme environmental conditions that occur as part of a major El Niño (Soto *et al.*, 2004).

Multiple sensory modalities in reunions

Female-initiated searches were characterised by multiple sensory modes. Spatial cues are used by females to find pups to some extent as they clearly remember which area of a large colony around 500 m long they left their pup. Pups do not wander far from their birth area until they are a few months old and they return to the area to reunite (pers. obs.). Pups also appear to use spatial cues, as they were sometimes observed to visit their mothers' favourite nursing rock while searching. These observations support studies by Dobson & Jouventin (2003) on Antarctic fur seals and Phillips (2003) on South American fur seals that found spatial memory does exist in mothers and pups. Visual cues also assist in searching, as the posture and movements of searching females (Stirling, 1971a), and the appearance of wet females, appear to attract the attention of pups. In contrast, calling females that were dry, and resting, did not have the same attraction, as few pups responded in these cases.

Vocalisations played a significant role in mother-pup reunions. They allowed recognition between mother and pup at distances of at least 26 metres and where the colony terrain impaired vision. The only reunions to occur without vocal cues were when either the mother or the pup left then returned to the other in the same location. Individual recognition of a female's pup-attraction calls resulted in no non-filial pups responding to the calling female in 49% of reunions despite her often being surrounded by pups. Even though up to seven non-filial pups responded to a searching female, many would cease calling after the first response and did not approach the female. Non-filial pups approached the searching female in only 20% of reunions and made contact with the female in 29% of reunions. This level of interaction is slightly higher than that observed for Californian sea lion pups, where only 9% of reunion

attempts involved non-filial pups approaching females (Gisiner & Schusterman, 1991). Variability among species in female discrimination by pups appears to be related to the risk of injury associated with approaching unrelated females (Insley, 2001). In New Zealand fur seals, risk of injury by females appears to be low (pers. obs.) and olfactory contact was used as confirmation of vocal recognition, sometimes used alone when females approached silent pups. In contrast, South American fur seal pups responded to the wrong female in only 18% of reunion attempts, which may be because the risk of being attacked by females is high in this species (Phillips, 2003). As vocalisations between mothers and pups were not always in response to the correct individual in this study, olfaction appeared to be the more reliable means of recognition. Occasionally females appeared to identify their pups solely on vocalisations but these were limited to a few cases of pup-initiated reunions where the female was resting.

Females appeared to be less motivated to reunite during onshore reunions, with fewer calls emitted by females during these reunions (Table 2), when compared with reunions after a foraging trip. This is probably because the female has already reunited with her pup that day prior to observation. During onshore reunions, more calls were emitted by females during successful reunions than unsuccessful reunions (Table 2). Resting females often called infrequently and did not move, resulting in many unsuccessful reunions. There were also onshore reunions where the female was not resting beforehand and that involved the female moving and calling, but unfortunately these reunion types were not distinguished. There was a difficulty in distinguishing between the onshore reunions that involved much calling and moving by females and offshore reunions because ridges and islands prevented many

observations of females coming ashore, and wet females could have been in tide pools rather than at sea. Furthermore, it could not be determined whether a female coming ashore had been away foraging or had been swimming near the shore, apart from females with radio transmitters but their reunion behaviour was not observed frequently enough to make any conclusion. Consequently, it was assumed that any wet female had returned from foraging and a dry female had become separated with her pup recently, which may have affected the results.

Asymmetrical behaviours of mothers and pups

Under parent-offspring conflict theory, it is expected that different selective pressures act on mothers and pups (Trivers, 1974). The finding that pups expended more effort (indicated by the number of calls) during reunions than females (Table 3) suggests that the motivation to reunite is greater for pups than for females. If a pup does not reunite, starvation will most likely result, whereas if a female does not reunite with her pup she may see a decrease in reproductive success. Furthermore, pups benefit by being liberal in their acceptance of females, as the benefit of gaining additional nutrition appears to outweigh the minimal risks of injury by unrelated females. Only 7.1% of non-filial pups were bitten by searching females and no injuries resulted. Some pups displayed submissive behaviours toward unrelated females before they were threatened, probably to counteract female aggression (pers. obs). Many pups were observed to accept unrelated females, only leaving when threatened and sometimes rather reluctantly. Some pups exhibited the excited behaviour seen when pups successfully reunite with their genetic mother (pers. obs.). Females appeared to more limiting in their pup-acceptance criteria. This was not experimentally tested, but there were few observations of females accepting non-filial pups for limited periods

and in most of these cases other factors were likely to be involved. Some females that did not reject non-filial pups immediately appeared to be distracted in responding to their approaching filial pups, and once reunion occurred, the non-filial pup was threatened or the mother-pup pair moved away. Other females appeared confused by two calling pups approaching at the same time and took longer to distinguish between the filial and the non-filial pup.

As pups grew older, reunions became more efficient. Search duration during female-initiated reunions decreased over time (Figure 8). The number of calls emitted (Figure 9) and the distance travelled by females also decreased with increasing pup age (Figure 10). Furthermore, the distance travelled by filial pups increased over time (Figure 11). These trends suggest that as pups become older and their ability to recognise and reunite with their mother becomes highly developed, they increase their reunion effort while females decrease their effort. Either the behaviour of the female changes, forcing the pup to make more effort, or pups could be more motivated to reunite as their nutritional needs increase and as foraging trip duration increases (Charrier *et al.*, 2002a). It is possible that the observed trend is an effect of pups travelling around more as they become older rather than an increased motivation of the pup or a behavioural change in the female. Pup searching behaviour did not change with age; however observations were only made over a period of 23 days.

Implications of maternal absence on pup searching behaviour

Pups made more effort to reunite when their mothers were present in the colony indicated by greater median number of searches, proportion of time searching, number of calls emitted and distance travelled, although only the number of calls was

significantly greater when mothers were present. This is not surprising as pups had most likely been with their mothers earlier and were attempting to locate her again. Pups may also have been calling in response to their mothers but this could not be determined in most cases because few females were identifiable and the colony terrain prevented identification of calling females. Pups responding to female calls appeared to call more frequently than pups calling spontaneously (pers. obs.). There was no significant relationship between search effort and the duration of maternal absence. However, searching behaviour of pups whose mothers were reliably identifiable was only observed between 1-4 days of maternal absence. Hunger would be expected to motivate pups to increase search effort, which may be the case when foraging trips are extended. Charrier *et al.* (2002a) found that pups did not alter begging behaviour until 5 days of maternal absence. The proximity of feeding grounds to this study colony of *A. forsteri* may not create a situation where pups are under high levels of nutritional stress. However, more milk stealing was observed when females were absent than when present (see Chapter 4). Pups should not expend a great amount of energy searching for females when there is no chance of reunion. However, pups may shift their rejection threshold and increase their frequency of response to unrelated females (Insley, 2001; Charrier *et al.*, 2002a). They may also exhibit more milk stealing behaviour rather than mother-searching behaviour, which could reduce their ability to successfully steal milk because of their calling (pers. obs).

In summary, mother-pup recognition in *A. forsteri* appears mutual but there is asymmetry in development and searching during reunions and this may be due to different selective pressures. Pups are more motivated to reunite because the cost of failed reunion is greater for pups than for females. Therefore, pups play a very active

role in the success of reunions compared to females. Low levels of aggression in this species also allow pups to be indiscriminating when responding to, and approaching, unrelated females, in order to have a greater chance of gaining nutrition. Apparent recognition errors on the part of the female were observed, under situations of female aggression and confusion, but none of these resulted in misdirected suckling. Pups would be expected to alter searching behaviour and effort when under nutritional stress during maternal absence. However, the short foraging trips of *A. forsteri* mothers at this colony appeared not to cause nutritional stress.

Chapter 3: Inter-Individual and Intra-Individual Variability of the Female-Attraction Call of New Zealand Fur Seal (*Arctocephalus forsteri*) Pups

Abstract

Efficient recognition between mothers and pups of the New Zealand fur seal (*Arctocephalus forsteri*) is essential for reunion following the frequent separations that occur due to maternal foraging. Pup vocalisations are important cues for females to find their pups and therefore need to be individualistic. This study investigated the individuality of ten acoustic variables of female-attraction calls of 12 pups recorded at Ohau Point, Kaikoura, New Zealand using several different tests of individuality. Pup calls were individualistic, with an average of 67% of calls correctly assigned to the caller by discriminant function analysis. Variables associated with the fundamental frequency and the frequency of the lowest harmonic were consistently the most stereotypic in the different tests. This study also investigated whether pup vocalisations differed when mothers were present to when they were absent from the colony. There was no difference in the acoustic features of vocalisations or the inter- and intra-individual variation in calls produced between maternal absence and presence. Intra-individual variation of one acoustic variable, associated with the frequency of the lowest harmonic, decreased over time during maternal absence. This may suggest that pups exhibit an alternative strategy whereby they emit modified vocal signatures to assist attempts at obtaining allomaternal care.

Introduction

The ability to recognise offspring is important for otariid pinniped females, as frequent foraging trips to sea and high mobility of pups result in frequent mother-pup separations. The often high density of otariid pinniped colonies, rocky terrain and high background noise increases the difficulty for females locating their pups (Page *et al.*, 2002; Charrier *et al.*, 2003c). Discrimination between filial and non-filial pups is an important aspect of maternal care, which prevents misdirected allocation of resources (McCulloch & Boness, 2000). Lactation is extremely costly for otariid females; therefore misdirected parental effort lowers reproductive success (Riedman, 1982). Pup survival also depends on mothers' recognition of pups, as otariid females will rarely feed non-filial pups (Stirling, 1975; Lunn, 1992). Recognition of mothers by pups is also essential because there is a risk of being bitten by unrelated females (Roux, 1986; Lunn, 1992). Thus, there is strong selection pressure for a reliable mother-pup recognition system that allows discrimination among individuals.

Recognition between mother and pup may be facilitated by visual, olfactory and acoustic cues (Phillips, 2003). Vocalisations are the only effective means of communication over short and long distances, and consequently, are the primary cue used by mother and pup to locate one another and reunite following separation (Insley *et al.*, 2003). For reliable acoustic recognition, female- and pup-attraction calls must be highly stereotyped, with the variation between individuals being greater than that within individuals (Trillmich, 1981; Insley, 1992; Phillips & Stirling, 2000; Charrier *et al.*, 2002b). Playback experiments have demonstrated sufficient call stereotypy for otariid females and pups to be more vocally responsive to calls of filial pups and

females compared to those of unrelated individuals (Insley, 2001; Charrier *et al.*, 2001a; Charrier *et al.*, 2002b; Charrier *et al.*, 2003a).

Studies on phocid female and pup vocalisations have found that they are individualistic (Insley, 1992; Job *et al*., 1995; Caudron, 1998; McCulloch *et al*., 1999; Van Opzeeland & Parijs, 2004) however given the poorer recognition abilities of phocids compared with otariids we would expect them to be less individualistic than calls of otariids (Insley, 1992).

Acoustic stereotypy of female- and pup-attraction calls has been quantified for most otariid species, including *Callorhinus ursinus* (Insley, 1992), *Arctocephalus gazella* (Page *et al.*, 2002), *A. galapagoensis* (Trillmich, 1981), *A. australis* (Phillips & Stirling, 2000), *A. tropicalis* (Charrier *et al.*, 2002b; Charrier *et al.*, 2003a,c), *Zalophus wollebaeki* (Trillmich, 1981) and *Otaria byronia* (Fernandez-Juricic *et al.*, 1999). New Zealand fur seal (*A. forsteri*) female and pup calls have been described and measured in several studies (Stirling, 1970; Stirling, 1971a; Stirling & Warneke, 1971), however statistical investigation of call individuality has only been undertaken once previously on *A. forsteri*, on the Otago Peninsula (Page *et al.*, 2002).

The methods frequently employed to investigate pinniped vocal individuality are a form of multivariate analysis such as principal components analysis to determine acoustic features contributing to variation of calls, and discriminate function analysis which gives estimates of individuality based on similarities between acoustic variables (Phillips & Stirling, 2000; Page *et al*., 2002). Charrier *et al*. (2003c) recommended using the potential of individuality coding in place of multivariate

analyses, to indicate the level of inter-individual variation relative to intra-individual variation for each acoustic variable. Variables that encode the most information about individual identity must have a greater inter-individual variation than intra-individual variation (Charrier *et al*., 2003c).

The female-searching behaviour of pups may be affected by environmental constraints, such as those placed upon pups during maternal absence (Charrier *et al.*, 2002a). Pups often appear to be indiscriminate towards females and are likely to nurse off any female that accepts them (Chapter 2; Insley, 2001). During maternal absence periods, pups must fast and in an attempt to gain additional nutrition under this stress, may increase attempts to steal milk (Ono *et al.*, 1987; Lunn, 1992). As with milk stealing attempts, the female-attraction calls emitted by pups should be signals of offspring hunger during maternal absence (Godfray, 1995). Subantarctic fur seal pups modify their begging behaviour during their mother's absence, responding more strongly to the calls of unrelated females after five days of maternal absence (Charrier *et al.*, 2002a). The vocal responses of pups toward unrelated females may be attempts to obtain allomaternal care.

Modifications in the vocalisations of pups may be apparent during maternal absence and linked to changes in their motivational state. Preliminary observations on distressed harbour seal (*Phoca vitulina*) pups found an increase in the number of calls per calling bout, a faster rate of call emission and a greater number of harmonics (Perry & Renouf, 1988). This appears to be the only research in any pinniped species investigating the effect of the pups' motivational state on the features of vocalisations.

New Zealand fur seal (*A. forsteri*) females at Kaikoura's Ohau Point seal colony leave their pups for relatively short foraging trips of 2-4 days (L. Boren pers. comm.), a result of a nearby food source (Carey, 1992). Despite this, pups often attempt to steal milk (see Chapter 4), indicating a level of nutritional stress which may affect their motivational state. Pups also respond vocally, to unrelated females which may be another strategy adopted by pups to gain allomaternal care (Charrier *et al*. 2002a).

In this study I examined the acoustic stereotypy of the female-attraction call of pups. I then compared these data to similar previous studies. I also investigated possible acoustic differences and intra- and inter-individual variation of calls emitted by pups during maternal absence and presence, under the hypothesis that pups may modify their vocal signatures during their mothers' absence.

Methods

Field work was carried out at Ohau Point seal colony, 26 km north of Kaikoura (42°3S/173°4E) on the east coast of the South Island, New Zealand (see Chapter 2 for a detailed description of the colony). Recording of vocalisations was undertaken during two austral summers from January-March 2004 and December 2004-January 2005. From here on, the first season will be referred to as 2004 and the second as 2005. Recording was undertaken in two sectors of the colony in 2004 that allowed access with minimal disturbance and provided the best locations for recording. Recording was reduced to one site in 2005, to gain a greater number of vocalisations for each pup in the shorter time frame available.

In 2004, 65 pups in both sectors were marked with a combination of numbered caps glued to their fur and flipper tags. VHF radio transmitters (frequency 160 MHz) were attached to 15 females in the two sectors to identify periods of maternal presence/absence. An omni-directional antenna, R2100 receiver and D5041 data logger were left at the centre point of the colony, programmed to scan the assigned frequencies every 30 minutes and record presence or absence of a signal. In 2005, 34 pups were marked in the one sector where recording took place. VHF radio telemetry transmitters were attached to 8 females. In both seasons these females were flipper-tagged or marked with numbered caps glued to fur to allow identification during daily behavioural observations.

Recording techniques

Recordings were made using a Marantz PMD670 digital solid state recorder with a frequency response of 20,000 Hz ±0.5 dB and a Sennheiser ME67 long gun microphone with a frequency response of 50-20,000 Hz ±2.5 dB, powered by a Sennheiser K6 battery power module. A Rycote full windshield system with modular windshield, modular suspension, windjammer and hi wind cover was used to reduce wind noise. Vocalisations were sampled at 44.1 kHz by the recorder and recorded in MP3 format onto compact flash card.

Female attraction calls emitted by marked pups were recorded opportunistically when they were searching for their mothers. The recordings were made between 1-15 metres from the focal pup without disturbing their behaviour. Pups' cap or tag numbers were noted while recording. I recorded vocalisations of any marked pup, but analysed only those from pups who had mothers for whom VHF telemetry data (therefore reliable presence/absence data) had been obtained.

Acoustic Analyses

Twelve pups had a sufficient number of vocalisations with measurable acoustic features for further analysis. A total of 243 calls were analysed, ranging from 10-31 for each pup. Calls were analysed from bouts of at least three calls, up to a maximum of ten calls from one bout. Calling bouts with fewer than three calls were considered insufficient to allow comparison with other bouts of greater numbers of calls (Charrier *et al.*, 2002b). Most calling bouts contained less than ten calls, but where there were more, I randomly selected ten calls to analyse, to reduce extreme differences in the sample sizes of calls between pups.

Vocalisations were converted to AIFF files. Spectral analyses were carried out using Canary version 1.2.4 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, USA). Calls were played into the computer at the rate given by seals, sampled at 44.1 kHz. Temporal and spectral characteristics were examined on spectrograms and power spectra after performing 512-point Fast Fourier Transforms (FFTs; time resolution 5.805 ms, frequency resolution 86.13 Hz) (Phillips & Stirling, 2000; Page *et al.*, 2002). Power spectra were averaged over the entire duration of the call.

I measured the acoustic variables described in Table 1 for each call, using the methodology of Phillips & Stirling (2000). Cursor precision was estimated to be ±1 ms and ±14 Hz, and ±0.3 dB and ±6 Hz, for spectrograms and power spectra, respectively. Only the continuous variables were subjected to statistical analyses.

Table 1. Description of acoustic variables measured from fur seal female-attraction calls by pups and their abbreviations (Phillips & Stirling, 2000).

Variable	Description of acoustic variable
TONAL	Presence/absence of tonality (harmonic structure) within a call
PULSE	Presence/absence of pulsing within a call
FM	Presence/absence of rhythmic frequency modulation within a call
DUR	Duration of call (ms)
NPARTS	Number of parts per call
HI	Harmonic interval (Hz)
INF	Frequency of lowest visible harmonic at onset of call (Hz)
MAXF	Maximum frequency of lowest visible harmonic (Hz)
ENDF	Frequency of lowest visible harmonic at end of call (Hz)
PEAK1	Frequency of first energy peak (Hz)
PEAK2	Frequency of second energy peak (Hz)
PEAK3	Frequency of third energy peak (Hz)
RAMP1	Ratio of amplitudes of the first and second energy peaks (%)
RAMP2	Ratio of amplitudes of the first and third energy peaks (%)
FMP	Period of rhythmic FM when present (ms)
FMR	Range of rhythmic FM when present (Hz)

Statistical Analyses

All analyses were made with SPSS for Windows 11.5 (SPSS Inc., Chicago, USA), except for the principal components analyses, which were made using Minitab Release 14 (Minitab Inc.).

Principal components analysis (PCA) with varimax rotation was used to investigate the acoustic variables contributing to the variation of calls (Phillips & Stirling, 2000). Factors with eigenvalues greater than one were accepted, as these explained more variation than a single variable.

Coefficients of variation (CV) were calculated for each acoustic variable for each pup as a measure of intra-individual variation. Measures of inter-individual variation were obtained by calculating the CV for each acoustic structure from the means for each individual. To assess the potential for individual identity coding (PIC), the ratio of inter-individual CV to intra-individual CV was calculated for each acoustic variable (Charrier *et al.*, 2003c). When the PIC value is greater than one, it indicates that the inter-individual variation is greater than the intra-individual variation so the acoustic variable may encode information about the caller's identity. Absolute differences in acoustic structures between pups were examined using a Kruskal-Wallis test (Phillips & Stirling, 2000; Page *et al.*, 2002; Charrier *et al.*, 2003c).

To further test individuality, a stepwise, linear discriminant function analysis (DFA) with a minimisation of Wilk's λ and a cross-validation test was utilised (Phillips & Stirling, 2000). DFA indirectly indicates variation between individuals by showing the proportion of calls that can correctly be assigned to a pup based on similarities

among acoustic variables. A Wilcoxon-signed ranks test was used to examine the difference between the numbers of correctly assigned calls in the DFA and those in the cross-validation test for each pup.

To investigate possible effects maternal absence and pups' state of hunger on female-attraction calls made by pups during searching, the differences in acoustic structures and within-individual CVs of acoustic structures between calls made during maternal absence and presence was investigated using Wilcoxon signed-ranks tests. DFA's were undertaken separately on calls made during maternal absence and those during maternal presence and the numbers of correctly assigned calls compared between the two for each pup using a Wilcoxon signed-ranks test.

To test for an effect of the duration of maternal absence on the intra-individual variability, Spearman's rank correlations were undertaken between within-individual CVs and the number of days since mothers' departure for each acoustic structure, with pups pooled by days of female absence. Correlation between inter-individual variability (between-individual CVs) and duration of maternal absence could not be tested because of small sample size. The effect of pup age and sex on the significant correlation between within-individual CVs and duration of maternal absence was tested. The relationship between pup age in days and CVs was tested using Spearman's rank-correlation. The difference in CVs between male and female pup calls was tested with a Mann-Whitney test.

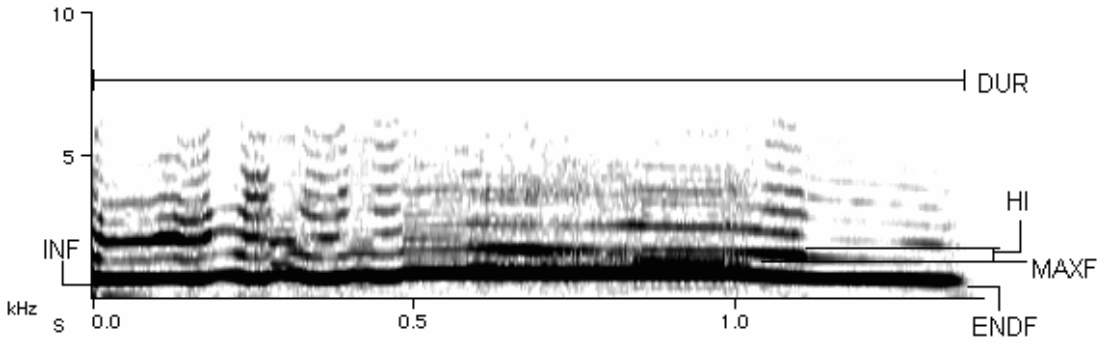
Results

Description of female-attraction calls by pups

Representative spectrograms and summary statistics of fur seal pup vocalisations are presented in Figure 1 and Table 2, respectively. The fur seal pups emitted calls that were mostly purely tonal (45%) or a combination of tonal and pulsed (45%) (Figure 2a, b). Many tonal and pulsed calls began with pulsed regions and ended with tonal regions. Some calls were also frequency modulated (Tonal + FM: 7%; Tonal + Pulsed + FM: 3%; Figure 2b, c). Three pups made staccato calls consisting of numerous brief pulses made in succession (Figure 2a). It appeared that energy peaks coincided with the harmonics in most calls, usually decreasing in intensity as frequency increased.

The number of parts per call varied from one, in purely tonal calls, to 39 in staccato calls. It appeared that the distinguishable number of parts decreased with increasing background noise, therefore this variable was not used in further analyses. FMP and FMR were not used in the analyses because of small sample sizes (n=22 calls for each variable).

a



b

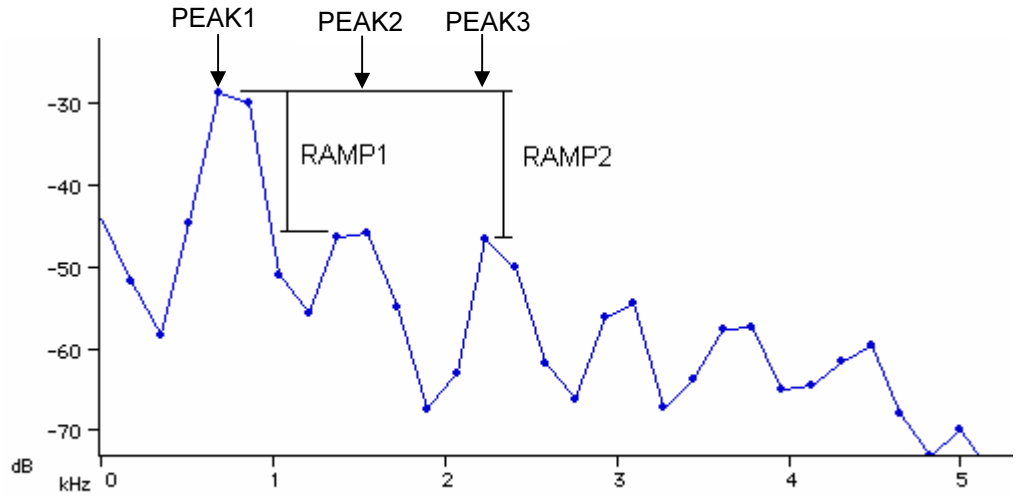


Figure 1. Representation of a tonal pup vocalisation, indicating acoustic variables measured a). spectrogram, with time (s) vs. frequency (kHz) b). power spectrum, with frequency (kHz) vs. amplitude (dB). See Table 1 for a description of measurements and their abbreviations.

Table 2. Summary of acoustic variables measured from female-attraction calls of pups (n = 12). All values are in Hz except DUR (ms), FMP (ms) and RAMP (%). Variables are defined in Table 1.

Variable	Grand mean	SE	Range	N
DUR	896	205	101-2171	234
HI	931	293	160-1985	234
INF	654	98	221-1283	230
MAXF	1153	136	795-1885	234
ENDF	684	97	370-1533	233
PEAK1	841	75	428-1204	234
PEAK2	2165	253	1032-3104	234
PEAK3	3366	393	1980-5258	227
RAMP1	77.9	7	56-119	234
RAMP2	72.5	5	55-102	227
FMP	33.4	17	8-76	22
FMR	490	126	307-1110	22

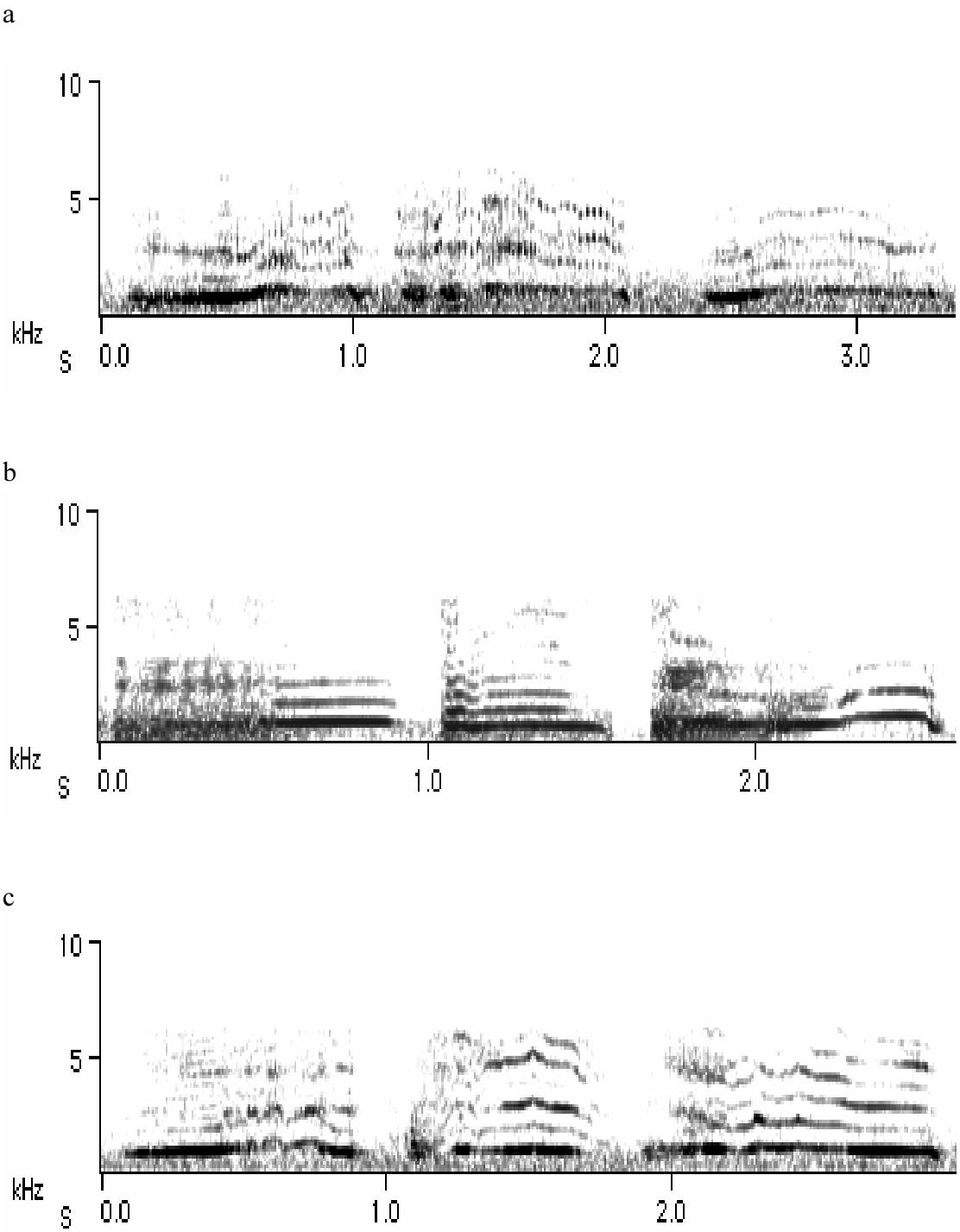


Figure 2. Spectrograms (frequency vs. time) of pup vocalisations showing intra- and inter-individual variation. Three calls each of three pups are shown. Note the difference in time scale for each spectrogram. a). Tonal and staccato calls. b). First and third calls tonal and pulsed, second call tonal and frequency modulated. c). Tonal and frequency modulated calls, with some pulsing near the beginning of the second and third calls.

Dimensionality of call variation

The principal components analysis (PCA) extracted three factors that explained 59% of the variance in the sample (Table 3). Frequency and temporal characteristics (PEAK2, PEAK3, HI and DUR) had their highest factor score loadings on the first factor and contributed to 22.7% of the variation of pup calls. Similarly, 19.9% of the variation was attributed to the characteristics of the lowest harmonic (PEAK1, INF, ENDF, MAXF) which loaded highest on the second factor. The amplitude variables, RAMP1 and RAMP2, explained a further 16.5% of call variation.

When two factors were extracted by the PCA, the acoustic variables describing the lowest harmonic (PEAK1, MAXF, INF, ENDF; in descending order of factor loadings) loaded highest on the first factor and explained 24% of the variation. All other acoustic variables loaded highest on the second factor, explaining 22% of the variation. These results show a clustering of calls within pups, indicating a low level of intra-individual variability compared to the greater level of variability between pups (Figure 3).

The results also indicate a disparity between the calls of female and male pups, particularly on the first factor which suggests that the lowest harmonic is generally of a different frequency than male pups (Figure 4). This was confirmed by Mann-Whitney tests between measurements of each acoustic variable for male and female pup calls. Calls of female pups had significantly greater frequency values than those of male pups (MAXF: W=18385, n=234, P<0.001; ENDF: W=17335, n=233, P<0.019; PEAK1: W=18704, n=234, P<0.001; PEAK2: W=18020, n=234, P=0.004; PEAK3: W=16434, n=227, P=0.002). INF, DUR, HI, RAMP1 and RAMP2 were not

significantly different between male and female pup calls (INF: W=16674, n=230, P=0.052; DUR: W=16338, n=234, P=0.810; HI: W=16897, n=234, P=0.181; RAMP1: W=14456, n=228, P=0.181; RAMP2: W=14023, n=227, P=0.062).

Table 3. Summary of principal components analysis (PCA) on acoustic variables for female-attraction calls of fur seal pups, showing rotated factor loadings of each variable on factors with eigenvalues greater than one (highest loadings for each variable indicated in bold).

Acoustic variable	Factor 1	Factor 2	Factor 3
PEAK2	**0.864**	-0.236	0.020
PEAK3	**0.792**	-0.286	-0.037
HI	**0.624**	-0.108	-0.074
DUR	**0.593**	0.188	-0.120
INF	-0.050	**-0.746**	-0.021
ENDF	0.012	**-0.681**	-0.075
PEAK1	0.224	**-0.672**	0.720
MAXF	0.208	**-0.569**	0.076
RAMP2	-0.034	-0.009	**-0.919**
RAMP1	0.250	0.092	**-0.863**
Eigenvalue	2.273	1.990	1.652
Variance explained	22.7%	19.9%	16.5%
Cumulative variance	22.7%	42.6%	59.2%

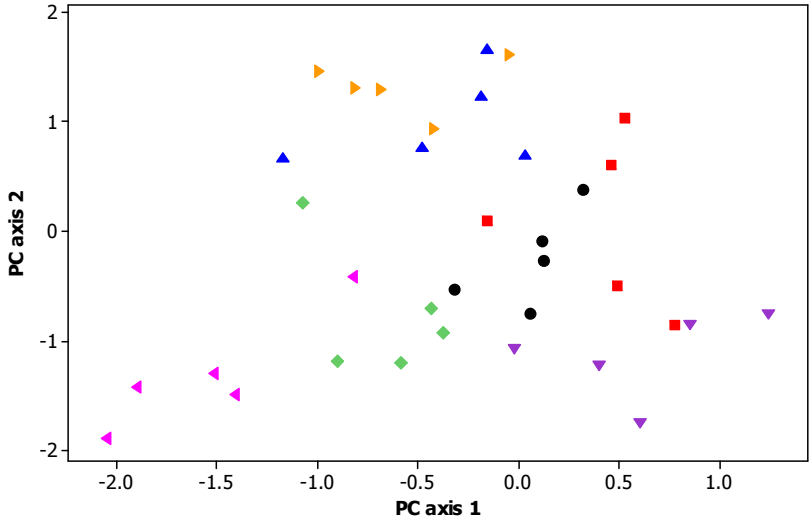


Figure 3. Individual pup calls plotted according to their principal components on two axes of factor scores, indicating inter- and intra-individual variability (n=5 pups, 5 calls for each). Each pup is represented by a different symbol and each call is a different point. PC axis 1 is related to the frequency characteristics of the lowest harmonic (PEAK1, MAXF, INF, ENDF), and PC axis 2 is related to all other frequency, amplitude and temporal characteristics (RAMP1, PEAK2, RAMP2, PEAK3, DUR, HI; in descending order of factor loadings).

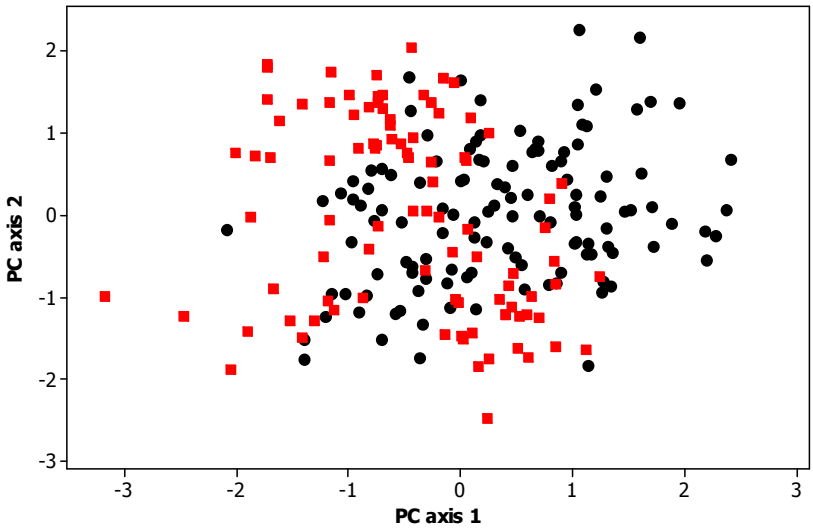


Figure 4. Gender difference in pup calls plotted according to their principal components on two axes of factor scores. Each call is a different point (n=217 calls). Females are represented as circles and males as squares. PC axis 1 is related to the frequency characteristics of the lowest harmonic (PEAK1, MAXF, INF, ENDF), and PC axis 2 is related to all other frequency, amplitude and temporal characteristics (RAMP1, PEAK2, RAMP2, PEAK3, DUR, HI). There is a general difference between the sexes on axis 1 indicating a difference in frequency characteristics of the lowest harmonic.

Inter-individual variation of pup calls

Potential for individual identity coding (PIC) values indicated that inter-individual variation was greater than intra-individual variation for the frequency characteristics of HI, MAXF, ENDF and PEAK1 (the latter three are characteristics related to the first harmonic), but this was not so for DUR, INF, PEAK2, PEAK3, RAMP1 and RAMP2 (Figure 5). However, Kruskal-Wallis tests indicated that all variables were significantly different between pups (Table 4).

The discriminant function analysis (DFA) indicated a high level of call individuality among pups. Calls were correctly assigned to individuals about 67% of the time, although some individuals were more distinguishable than others (Table 5). The lowest classification rates were still much higher than would be expected by chance (i.e. for 12 pups, 1/12 = 8.3%). Classification rates of calls of male and female pups did not differ significantly (Mann-Whitney, W=39, n=12, P=0.330). The variables PEAK3 and RAMP2 were not extracted by the DFA. PEAK1 (R=0.65) and MAXF (R=0.62) were strongly correlated with the first function, while HI (R=0.70) was correlated with the second function, with the first two functions accounting for 59% of the variation between pups. The results indicate that these variables that contain information about the frequencies of the lowest harmonics were used to discriminate between calls by the DFA suggesting they are the most stereotypic variables.

The cross-validation test correctly assigned pup calls about 59% of the time (range 29-83%) and these classification rates for each pup were significantly less than the DFA (Wilcoxon signed-ranks: Z=-2.701, df=11, P=0.007). However, all pups were

still classified at higher rates than expected if they were distributed randomly (8.3% classification rate).

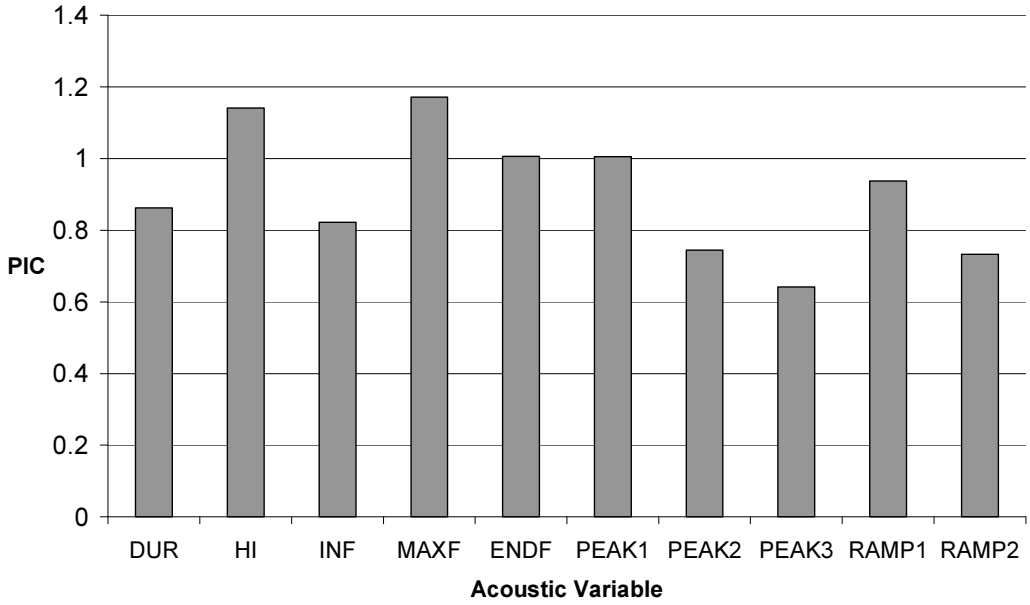


Figure 5. Potential for individual identity coding (PIC) values for ten acoustic variables of pup calls. PIC values >1 indicate that inter-individual variation is greater than intra-individual variation.

Table 4. Results of Kruskal-Wallis test among pups of acoustic features of pup calls. All tests significant at $P<0.001$ (df=11).

Acoustic variable	Kruskal Wallis *H*	n
DUR	107.3	234
HI	114.1	234
INF	72.3	230
MAXF	134.4	234
ENDF	100.3	233
PEAK1	118.6	234
PEAK2	81.0	234
PEAK3	67.7	227
RAMP1	91.7	228
RAMP2	61.0	227

Table 5. Classification of calls to individual pups based on discriminant function analysis, arrange in descending order of classification rate (%). Calls that were assigned correctly are indicated in bold type.

				Pup to which calls were assigned												
Pup	Sex	*n*	%	112	116	4	103	11	86	14	55	101	26	59	21
112	M	13	92.3	**12**	-	-	-	1	-	-	-	-	-	-	-
116	M	18	88.9	-	**16**	-	-	-	1	-	-	-	-	-	1
4	F	22	81.8	-	-	**18**	-	-	-	1	-	-	-	-	3
103	M	30	80.0	1	-	-	**24**	-	-	1	-	2	-	2	-
11	F	16	75.0	1	-	-	-	**12**	-	-	2	-	-	-	1
86	F	13	69.2	-	2	-	1	-	**9**	-	-	1	-	-	-
14	F	16	68.8	-	-	-	1	1	-	**11**	1	-	1	-	1
55	F	22	68.2	-	3	-	1	-	-	-	**15**	-	1	1	1
101	M	15	66.7	1	-	1	2	1	-	-	-	**10**	-	-	-
26	M	18	44.4	-	1	2	-	-	1	3	2	-	**8**	-	1
59	F	10	40.0	-	-	-	2	-	2	-	2	-	-	**4**	-
21	F	31	32.3	1	3	6	-	3	-	1	3	2	2	-	**10**
N, $\bar{X}$		218	67.3												

Intra-individual variation of pup calls with maternal absence

There was no difference between the acoustic variables of calls for each pup when their mother was present and when she was absent (Table 6). There was also no difference between the coefficients of variation (CV) of calls within pups when mothers were absent and present (Table7).

The discriminant function analyses correctly assigned 77.1% of pup calls when the mother was absent (n=50) and 68.0% of calls when she was present (n=48). The difference in the counts of correctly assigned calls between the DFA's for calls emitted by pups during maternal absence and presence was not significant (Wilcoxon signed-ranks, Z=0.707, n=7, P=0.480).

There was a significant correlation between the number of days absent and the intra-individual CVs for the acoustic variable PEAK1 (r_s=-0.522, n=18, P=0.026; Figure 6). The other nine acoustic variables were not correlated with the number of days of maternal absence (DUR: r_s=-0.142; HI: r_s=0.064; INF: r_s=-0.271; MAXF: r_s=-0.088; ENDF: r_s=-0.138; PEAK2: r_s=-0.213; PEAK3: r_s=-0.281; RAMP1: r_s=-0.153; RAMP2: r_s=-0.098; all NS, n=18). The intra-individual CV of PEAK1 for pup calls were not affected by neither pup age (Spearman's rank correlation, r_s=0.063, n=31, P=0.736) nor pup sex (Mann-Whitney, H=0.05, df=1, P=0.828).

Table 6. Results of Wilcoxon-signed ranks tests comparing median values for each acoustic variable when the mother is absent vs. mother is present for each pup (n=7). All values are in Hz except for those of RAMP1 and RAMP2 (%). All tests not significant at $P>0.05$.

Acoustic variable	Present	Absent	*Z*	*P*
DUR	952	954	-1.183	0.237
HI	853	973	-1.338	0.735
INF	614	522	-1.352	0.173
MAX	1153	1090	-0.169	0.886
END	636	670	-0.676	0.499
PEAK1	859	864	-0.135	0.893
PEAK2	2242	2239	-0.314	0.753
PEAK3	3013	3447	-0.169	0.866
RAMP1	76	81	-1.014	0.310
RAMP2	72	75	-0.676	0.499

Table 7. Results of Wilcoxon-signed ranks tests comparing median coefficients of variation (CV) for each acoustic variable when the mother is absent vs. mother is present for each pup (n=7). All tests not significant at $P>0.05$.

Acoustic variable	Present	Absent	*Z*	*P*
DUR	30.3	23.4	-1.690	0.091
HI	14.8	18.0	-0.676	0.499
INF	18.6	16.4	-0.169	0.866
MAX	7.8	6.9	-0.676	0.499
END	13.5	15.0	-0.507	0.612
PEAK1	5.8	14.0	-1.859	0.063
PEAK2	18.1	12.1	-0.169	0.866
PEAK3	15.8	20.9	-1.183	0.237
RAMP1	5.5	9.1	-1.521	0.128
RAMP2	9.6	7.8	-0.338	0.735

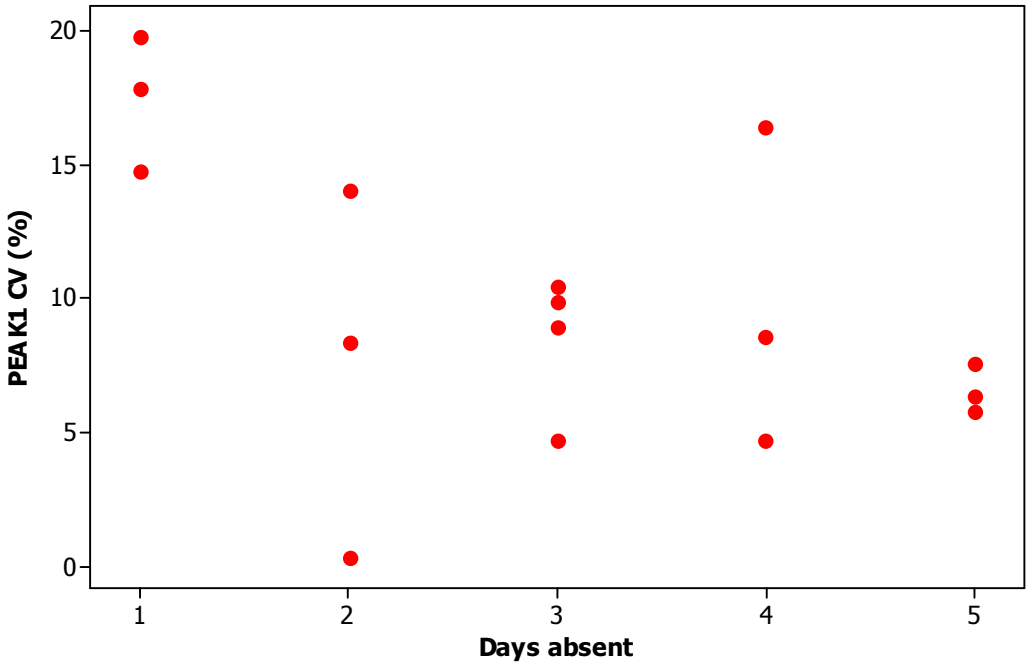


Figure 6. Significant correlation (r_s=-0.522, n=16, P=0.026) between the within-individual coefficient of variation (CV) of the acoustic variable PEAK1 of pup calls and the number of days the mothers had been absent. Pups were pooled by the number of days absent (n=10 pups).

Discussion

Individuality in the female-attraction call of pups

The female-attraction call of New Zealand fur seal (*Arctocephalus forsteri*) pups at Ohau Point seal colony, Kaikoura appears to show acoustic individuality. This study supports the results of Page *et al.* (2002) who studied *A. forsteri* on Otago Peninsula by providing further evidence of acoustic stereotypy in this species. It is also consistent with studies on other pinniped species that have shown individualistic female-attraction calls of pups (Trillmich, 1981; Insley, 1992; Job *et al.*, 1995; Caudron, 1998; Fernandez-Juricic *et al.*, 1999; McCulloch *et al.*, 1999; Phillips & Stirling, 2000; Charrier *et al.*, 2002b; Page *et al.*, 2002; Van Opzeeland & Van Parijs, 2004).

The different methods of testing individuality identified different acoustic features that are likely to encode the most information about callers' identity. The principal components analysis suggested that frequency characteristics such as the harmonic interval (fundamental frequency) and frequencies of the higher harmonics, as well as the duration of calls, accounted for most variation between pups, explaining 23% of call variation (Table 3). Frequency characteristics of the lowest harmonic explained 20% of variation in calls among pups (Table 3). It appeared that the calls of some pups exhibited greater levels of intra-individual variability than others, but overall inter-individual variation was greater than intra-individual variation (Figure 3). Potential for individual identity coding values demonstrated that variation among pups was greater than that within pups, for the acoustic variables of HI, MAXF, ENDF and PEAK1 only (Figure 5). As components of vocal signals that are used as

signatures must exhibit low intra-individual variability and relatively high variation among individuals, the PIC values suggest that variables associated with the fundamental frequency (HI), frequency of the lowest harmonic (MAXF, ENDF) and frequency of the first energy peak (PEAK1; which usually coincided with the lowest harmonic) may be used by mothers to recognise calls of their pups. The Kruskal-Wallis tests of absolute differences in each acoustic variable among pups indicated that all variables tested were highly individualistic (Table 4). This suggests that a combination of frequency, temporal and amplitude-related characteristics may be used by females to discriminate between the vocalisations of pups. The discriminant function analysis also indicated that discrimination between pups was possible based on linear combinations of acoustic variables, with those variables describing the frequency of the lowest harmonic (MAXF, PEAK1) and the fundamental frequency (HI) contributing to 59% of variation among pups.

Although these different methods of testing individuality suggested different degrees of stereotypy of acoustic features, the common result was that frequency variables were the most stereotypic, especially those variables relating to the lowest harmonic and the fundamental frequency. This is consistent with other pinniped studies in which characteristics of the fundamental frequency contained the best signatures for pup identity (Fernandez-Juricic *et al.*, 1999; Phillips & Stirling, 2000; Charrier *et al.*, 2002b). Call duration varied greatly within and among individual vocalisations, making it impossible to be used as a signature of the caller's identity. Similarly, frequency modulation was only present in a small proportion of pup calls (8%) and was present in only a few calls of each pup, indicating that it must not be necessary for recognition. However, it has been shown for other otariids that when present,

frequency modulation is useful for individual identity (Charrier *et al.*, 2002b). Calls with frequency modulation are highly directional, assisting in locating a calling individual, especially in a noisy environment (Charrier *et al.*, 2001b). Repeated pulses such as in staccato calls may also aid in localising the sender (Marler, 1955). The spectral energy pattern of higher frequencies and the amplitude pattern may also be useful for individuality, but to a lesser extent than other acoustic features.

Analyses of pup calls can be used to discover which acoustic features are stereotypic and therefore are likely to be used by females to recognise their offspring. However, pup vocalisations of some phocid species have been found to be individualistic but despite this there is a lack of maternal recognition (Caudron, 1998; McCulloch *et al.*, 1999). Behavioural observations of *A. forsteri* reunions indicated vocal recognition between mother and pup (this study; see Chapter 2). Playback experiments, which were beyond the scope of this work, would be useful to confirm the use of these stereotypic features in recognition of *A. forsteri* pups by their mothers (Charrier *et al.*, 2002b).

Pup calls were assigned to the right pup 67% of the time using discriminant function analysis (DFA). This result is comparable to the study by Page *et al.* (2002) on *A. forsteri* at Otago Peninsula where 79% of calls assigned to the correct pup. The sample size (10 pups) used in Page *et al*. (2002) was similar to that used in this study (12 pups), however in both studies the sample size was small. In this study, the DFA classified calls at different rates among pups (32-92%), which indicates that some pups are more distinctive than others so it is possible that the pups in the study by Page *et al*. (2002) were more distinctive. However, the lower rate of correct

assignment observed in this study could have been attributed to a difference in levels of individuality of pup calls between the study sites due to different selective pressures, as was observed in grey seals between two colonies with different topographies (McCulloch & Boness, 2000). In that study, playback experiments indicated that mother-pup recognition was present in the beach colony but absent in the boulder colony and it was suggested that mothers and pups in the boulder colony use olfactory and spatial cues rather than vocalisations to locate each other (McCulloch & Boness, 2000). *A. forsteri* inhabits rocky coastlines in both areas, and selection for efficient mother-pup reunions must be strong for both so it appears that selective pressures do not differ between Ohau Point and Otago Peninsula.

Another more likely explanation for the difference is that lesser-quality recordings were obtained for this study. Ohau Point colony was not the best colony of choice for recording vocalisations as it is exposed to strong winds and rough seas, and although the recording system reduced wind noise picked up by the microphone, wave noise was often high. Additionally, I was only able to record from the edge of the colony so as not to disturb the seals, but the pups spend most of their time in and around a tide pool and on an island near the sea's edge. I selected the best recordings for analyses, but some amount of background noise was unavoidable.

The classification rate (67%) is also within the range observed for other studies of otariids where sample size was comparable: *A. australis* (60%; Phillips & Stirling, 2000), *Callorhinus ursinus* (79%; Insley, 1992), *A. tropicalis* (83%; Page *et al.*, 2002) and *A. gazella* (52%; Page *et al.*, 2002). The differences between species may reveal differing selective pressures due to altered maternal foraging patterns and periods of

maternal investment between species (Miller, 1991; Page *et al.*, 2002). For example, the shortened lactation of *A. gazella* compared with other fur seals may result in reduced selection for highly individualised vocalisations (Page *et al.*, 2002). It has also been suggested that the tendency of *A. forsteri* and *A. tropicalis* to breed on rocky coastlines may result in a greater need for vocal stereotypy, over visual cues, when compared to *A. gazella* which breed on open beaches (Page *et al.*, 2002). However, the high rate of classification of *C. ursinus* pup calls found by Insley (1992) contradicts both of these hypotheses because this species also breeds on open beaches and has a reduced lactation length yet has high rates of vocal stereotypy. Nontheless, different selective pressures may act upon each species in the different locations to determine the level of individuality.

The findings that classification rates for phocid species are generally lower than those for otariids supports the findings of poor recognition abilities of pups by females (Caudron, 1998; McCulloch *et al*., 1999). Calls of *Mirounga angustirostris* pups were correctly assigned on average 64% of the time (Insley, 1992), *Leptonychotes weddellii* pup calls allowed a classification rate of 56% (Collins *et al.*, 2005), while *Phoca vitulina* pup calls were correctly classified 29% of the time (Khan, 2004). This is consistent with observations of more highly developed mother-pup recognition systems in otariids compared with those of phocids most likely due to the maternal strategy of otariids resulting in a greater number of separations (Insley, 1992).

Alternative begging strategies during maternal absence

Pups are subjected to frequent fasting periods, which are brief in *A. forsteri* at Ohau Point (average 2-4 days; L. Boren pers. comm.) in comparison to other otariid species

(2-3 weeks in *A. tropicalis*; Georges & Guinet, 2000; and 7-8 days in *C. ursinus*; Bartholomew, 1959). Despite maternal absence periods being short, pups will often attempt to steal milk in attempt to gain additional nutrition while females are absent (see Chapter 4; Lunn, 1992). This suggests a need for sustenance that provides benefits that outweigh the risk of being bitten when approaching unrelated females. However, low aggression levels exhibited by females toward pups in *A. forsteri* (see Chapter 2, 4) appear to allow pups to approach unrelated females more frequently.

Like milk stealing behaviour, the vocal responses of pups to calling females, or begging (Charrier *et al.*, 2002a), should honestly convey offspring hunger (Godfray, 1991; Godfray, 1995). Under parent-offspring conflict theory, selection acts on offspring to extract extra resources from parents but vocalising and moving toward females is energetically costly for pups (Trivers, 1974; Godfray, 1995). Charrier *et al.* (2002a) found that subantarctic fur seal (*A. tropicalis*) pups increasingly respond to female calls over time during maternal absence. It was also found that pups were increasingly vocally responsive to unrelated females from 5-11 days of maternal absence. This suggests that pups beg to unrelated females when under nutritional stress during the fasting periods of maternal foraging absences (Charrier *et al.*, 2002a). Non-filial *A. forsteri* pups were observed to respond to calling females in 51% of female-initiated reunion attempts (Chapter 2) and this could be an alternative strategy to milk stealing behaviour for gaining allomaternal care. In phocids, begging pups are sometimes accepted and nursed by unrelated females (Fogden, 1968), but in otariids, female recognition of their pups is well-developed so it would be expected that begging by otariid pups to unrelated females would be futile. However, cases of

fostering have been observed in *A. forsteri* (Chapter 4; Haase, 2004; S. McConkey, pers. comm.).

There is a possibility that pups modify their vocal signatures (Perry, 1988) and perhaps attempt to imitate calls of nearby vocalising pups in order to attempt to gain allomaternal care from unrelated females. This study appears to be the first to attempt to specifically investigate this possibility in otariid pups. However, there were no differences found for both the absolute values and the intra-individual coefficients of variation of the acoustic features of pup calls emitted between maternal absence and presence. The DFA assigned a greater (but not significantly greater) number of calls when the mother was absent, suggesting calls became slightly more individualistic among pups when mothers were absent which is the opposite of that expected if pups were imitating others' calls, which could result in reduced inter-individual variability. Similarly, the significant finding of decreasing intra-individual variation of the frequency of the first energy peak (which usually coincided with the lowest harmonic) of pup calls over time during maternal absence (Figure 6) is the opposite to that expected under the hypothesis of imitation of other pups' calls. Intra-individual variation would likely increase if pups were imitating calls of numerous other pups in different areas. However, pups congregate in pods around tide pools and this may cause vocalisations to converge on one form. The test contained low power due to a small sample size, but suggests that pups may reduce the variability of the frequency of the lowest harmonic of calls over time during maternal absence. As frequency characteristics, especially of the lowest harmonic appeared to be the most stereotypic therefore encode the most information about individual identity, modifications in this

call feature by pups may facilitate females accepting the approaches of vocalising non-filial pups.

There were a few cases of pups appearing to alter their vocalisations when numerous other pups were calling, but these changes may indicate increases in intensity of calls in order to compete with other pups searching for females. Changes in pup calls may also be affected by whether they were in response to female calls or not. This data was obtained in 2005 but not 2004. Future studies should investigate the likelihood of modification of pup vocalisations during maternal absence and call imitation more thoroughly by obtaining detailed behavioural observations of simultaneously calling pups responding to females or calling simultaneously to accompany recorded vocalisations. Larger sample sizes for each day since females' departure date would allow investigation of the association between inter-individual variation of call features and the period of pup fasting. Playback experiments would be useful in ensuing studies, using both recordings of female calls and other pup calls to investigate the effects of other calling individuals on the stereotypy and variation of pup vocalisations.

Chapter 4: Allosuckling and Rearing Two Pups to Weaning in the New Zealand Fur Seal *Arctocephalus forsteri*

Abstract

Allosuckling is often considered to be misdirected parental care. In pinnipeds it should be selected against because of the considerable costs of lactation unless there are additional benefits that may outweigh the costs. This study investigated occurrences of milk stealing, where females unknowingly feed non-filial pups, and fostering, where females are aware non-filial pups are nursing, in the New Zealand fur seal, *Arctocephalus forsteri* at Ohau Point, Kaikoura, New Zealand. During two breeding seasons, four cases of fostering were observed, two being long-term ('adoption') and two being less than a few hours each. For the adoption cases, both the fostered pup and filial pup of each female were of significantly lower mass, condition and growth rates than other pups in the colony. The female in one case reared both the filial and foster pups to weaning, but did not appear to spend a different amount of time ashore compared to females nursing single pups. Kin selection may have played a role in this case, as the foster pup was highly related to the filial pup. The total number of milk stealing attempts observed was 103 (an 8-13% frequency of marked pups), with a 14% success rate. Pups attempted milk stealing significantly more often during maternal absence than while their mothers were present. Mass and condition of some milk stealing pups fell outside confidence intervals for non-milk stealing pups. A review of fostering in pinnipeds reveals over 80 occurrences in otariids, with lower frequencies of fostering than those in phocids. This research is significant because it indicates that fostering exists in otariids, albeit at low frequencies despite the well-developed recognition system and the costs involved.

Introduction

Many species of pinnipeds are highly gregarious breeders (Riedman, 1982). Large numbers of individuals often gather in often limited pupping space and sometimes in harsh conditions. These situations provide ideal conditions for allosuckling, or the nursing of non-filial pups by females, to occur. Allosuckling in pinnipeds was traditionally thought to be an extremely rare occurrence (Marlow, 1972; Stirling, 1975). However, it has been studied both quantitatively and anecdotally, and found to be more widespread (Boness *et al*., 1992; Arnbom *et al*., 1997; Georges *et al*., 1999; Gelatt *et al*., 2001). There are two forms of allosuckling: fostering, where a non-filial pup is nursed by a female aware of the pup's presence, and milk stealing, where a female remains unaware of the nursing or rejects the non-filial pup as soon as it is discovered (Lunn, 1992).

There are anecdotal accounts of milk stealing (Reiter, 1978; Roux, 1986; Porter & Trites, 2004), however few studies have quantified the incidence of milk stealing (Lunn, 1992). It appears to be dependent on environmental conditions and nutritional stress (Ono *et al*., 1987; Lunn, 1992). Pups may become nutritionally stressed when they have become separated from their mother for long periods during adverse weather (Boness *et al*., 1992) or while mothers are away on foraging trips (Lunn, 1992). In such circumstances pups may seek additional nutrition or immunological benefits by nursing from more than one female (Roulin & Heeb, 1999). Pups risk being attacked and wounded by females during milk stealing attempts but this may be a small risk in comparison to the risk of starvation (Roux, 1986; Lunn, 1992).

Fostering has been reported in several phocid species that breed in large colonies but is a reportedly rare occurrence in otariids (Stirling, 1975; Trillmich, 1981; Riedman, 1982; Lunn, 1992). Lactation in pinnipeds is costly for mothers (Clutton-Brock *et al*., 1989), more so in otariids with their extended period of lactation (Oftedal *et al*., 1987). The nursing of non-filial young should be selected against unless there are reproductive benefits provided to the female that outweigh the costs of fostering. Kin selection may have a role in the occurrence of fostering whereby an individual's inclusive fitness is increased (Hamilton, 1964; Gemmell, 2003), however some studies have found no evidence of this (Perry *et al*., 1998; Schaeff *et al*., 1999). Other hypotheses propose that females may need to evacuate surplus milk (Roulin, 2002) or maintain the concentration of the neurohormone prolactin to enhance immunocompetence (Roulin, 2003). Also, females may foster pups to gain maternal skills, as many inexperienced females who have lost their pup adopt another non-filial pup (Riedman & Le Boeuf, 1982; Boness *et al*., 1992; Schaeff *et al*. 1999; Roulin, 2002). This may be particularly valuable to female pinnipeds, which are characterised by an energy-intensive and prolonged period of parental investment and a limited lifetime reproductive potential (Riedman, 1982).

Perhaps the most common explanation of fostering is recognition error (Riedman, 1982; Roulin, 2002). Recognition systems are highly developed in otariids, because of the need for females to leave their pups in large and dense colonies and then relocate them over an extended period of lactation (Riedman, 1990; Insley, 2001; Charrier *et al*., 2003b; Dobson & Jouventin, 2003; Phillips, 2003). A recognition system exists in phocids (Insley, 1992; Van Opzeeland & Van Parijs, 2004) but appears to be less developed than that in otariids because of the low degree of discriminatory nursing

behaviour of females towards non-filial pups (Fogden, 1968; Boness, 1990; Job *et al*., 1995). Phocids have a shortened lactation period compared with otariids that may not allow or provide the need for a well-developed recognition system (Kovacs, 1995). Furthermore, pups of ice-breeding phocids are well dispersed and relatively stationary suggesting that spatial cues are a primary means of reunion and well-developed recognition abilities are not essential (Kovacs, 1995). However, frequent separations of phocid mother-pup pairs in dense colonies due to inclement weather or disturbance may cause high levels of fostering (Fogden, 1971; Stirling, 1975; Boness *et al*., 1992). The relatively poor recognition abilities of phocids may explain the higher frequencies of fostering observed in these dense phocid colonies compared to otariids (Fogden, 1971; Riedman & Le Boeuf, 1982; Boness, 1990; Job *et al*., 1995; McCulloch *et al*., 1999). In phocids, fostering has been observed in frequencies up to 90% (Hawaiian monk seal, *Monachus schauinslandi;* Boness, 1990) whereas in otariids the highest fostering frequency observed was 11% (Antarctic fur seal, *Arctocephalus gazella*; Gemmell, 2003).

The success of otariid females rearing two pups to weaning is rare, having only been well described in three species: Antarctic fur seals, *Arctocephalus gazella* (Doidge, 1987), subantarctic fur seals, *A. tropicalis* (Bester & Kerley, 1983; Georges *et al*., 1999) and New Zealand fur seals, *A. forsteri* (Haase, 2004). For pups of mothers provisioning for two pups, growth rates were reduced in both Antarctic fur seals (Doidge, 1987) and subantarctic fur seals (Georges *et al*., 1999) from those observed for pups of mothers provisioning for singletons. Weaning was later for foster-filial pup dyads than for pups raised singly (Georges *et al*., 1999; Haase, 2004). Subantarctic fur seal females with two pups spent less time ashore (Georges *et al*.,

1999) whereas Antarctic fur seal females with two pups showed no difference in attendance or foraging trip duration than females with single pups (Doidge, 1987). New Zealand fur seal females with two pups on Kangaroo Island, Australia spent more time ashore and less time at sea (Haase, 2004).

Twinning is extremely rare in pinnipeds (Spotte, 1982). There are several cases of twin foetuses but it appears that twins are rarely born live (Vania, 1965; Bryden, 1966; Rae, 1969; Spotte, 1982; Ling, 1986; Barlough *et al*., 1987; Calkins & Goodwin, 1988; Fay *et al*., 1991). As a result, a female observed with two pups is sometimes assumed to be fostering one of them (Childerhouse & Gales, 2001). It, however, is also often assumed that observations of females nursing two pups are cases of twinning because fostering was thought to be nonexistent in otariids (Bester & Kerley, 1983; Doidge, 1987). Molecular studies provide evidence that mother-pup associations are not a reliable method of distinguishing between twinning and fostering whereas finding relatedness through microsatellite genotyping is a reliable method (Miller, 1971; Gelatt *et al*., 2001; McMahon & Hindell, 2003).

In this study, four cases of fostering were found in the New Zealand fur seal *A. forsteri*, which are among the first reported fostering cases in this species. Two involved the adoption of an additional pup, which were confirmed fostering cases through DNA genotyping. I examine the extent and the costs involved with milk stealing and fostering in *A. forsteri*, with reference to the occurrence and frequency of fostering in otariids and other pinnipeds.

Methods

All field work was carried out at Ohau Point seal colony (42°3S/173°4E), 26 km north of Kaikoura on the east coast of the South Island, New Zealand (see Chapter 2 for a detailed description of the colony). Field work was undertaken during two austral summers from November 2003-April 2004 and November 2004-January 2005. From here on, the 2003/4 and 2004/5 seasons will be referred to as 2003 and 2004, respectively. In 2003, 170 pups were marked with a combination of haircuts, numbered caps glued to their fur and flipper tags. In addition, we attached VHF radio telemetry transmitters to 19 females to identify periods of maternal presence/absence, and these females were tagged or had numbers glued to fur. An omni-directional antenna, R2100 receiver and D5041 data logger were left at the centre point of the colony, allowing signals to be picked up throughout the colony at 30 minute intervals. In total, there were 75 females identifiable from new and old tags and natural markings for the 2003 season. In 2004, 62 pups were marked, 12 females were tagged and around 120 females were identifiable based on prior tags or natural marks. VHF radio telemetry transmitters were attached to 14 females. The number of marked pups was reduced from the previous season because there were fewer projects requiring marked pups. Marked pups were caught and morphometric data (mass, axillary girth and standard dorsal length) were obtained every few weeks during both breeding seasons plus an extra set obtained around weaning time, in October 2004.

Behavioural observations

Instances of fostering and milk stealing were observed opportunistically through many different forms of behavioural data collection. Seal surveys were conducted

throughout the entire colony up to three times daily between 12 December 2003 and 9 February 2004 and twice daily between 15 November 2004 and 27 January 2005. The purpose of these surveys was to observe correct and incorrect associations (possible fostering events) of identifiable mother-pup pairs and to observe the presence and absence of known females. Pup behaviour, in terms of presence and absence of mothers and nursing times was recorded using scan sampling (Altmann, 1973) at 15 minute intervals in one area of the breeding colony between 10 December 2003 and 14 January 2004, and 11 December 2004 and 28 January 2005. Observations of births and mother-pup behaviour were conducted throughout the colony from 29 November 2003 - 6 March 2004 and 24 November 2004 - 28 January 2005.

A milk stealing attempt was defined as occasions when a pup silently (without vocalising) approached a female's belly or hind quarters in an attempt to gain milk. The attempt ended when the pup was driven away by the female or moved away on its own accord. A pup returning to another female or the same one was referred to as the second attempt. Milk stealing attempt bouts were defined as one or a number of consecutive attempts until the pup went out of sight or refrained from making any more attempts for five minutes. Milk stealing successes were defined as such, when a pup was visibly observed to be suckling without the female being aware of its presence. Fostering was only referred to as such when a non-filial pup was suckling from a female, aware of its presence but with no visible negative reaction from the female. Allosuckling was defined as all situations in which females nursed non-filial pups, whether milk stealing successes or fostering.

Skin and hair sampling

In 2003 I observed two females, each feeding two pups each. In one case an unmarked female was feeding two pups marked 'X6' and 'X7' and in the other case an unmarked female was feeding an unmarked pup and a pup marked with a diamond (from here on referred to as 'Diamond'). DNA samples were obtained from both females and all four pups to determine if they were incidences of fostering or twinning. Pups were caught and skin biopsies obtained from the trailing edge of fore flippers with piglet ear notch pliers (Majluf & Goebel, 1992). Hair samples were obtained from the two females at a distance using a modified crossbow and dart with a sticky disc attached to pick up follicles from the fur of the females (Caudron *et al*., in prep.).

DNA Analyses

DNA was extracted from skin samples using a modification of the protocol of Walsh *et al*. (1991) (Caudron *et al*., in prep.; Negro & Gemmell, in prep.). A $2mm^2$ tissue sample was suspended in 150 µl of digest ion buffer containing 5% Chelex 100 (7.5 g Chelex 100; 3 ml 5M NaCl; 7.5 ml 1M Tris, pH 8.0; 7.5 ml 20% SDS; 3ml 0.5M EDTA; dilute to 150 ml with ddH_2O). Proteinase K (10mg/ml) and 10mg/ml of RNase was added to final concentration of 100mg/ml (1.8 µl of each). The sample was incubated for 2-3 hours at 50°C and then spun at 15,300 x g for 1 minute. The supernatant was transferred to a new tube containing a buffered Chelex solution (7.5 g Chelex 100; 1.5 ml 1M Tris, pH 8.0; 300 µl 0.5M EDTA; dilute to 150 ml with ddH_2O). The sample was then spun at 15,300 x g and stored at -20°C. Prior to use the sample was spun and the supernatant was retained. Microsatellite amplification, separation of amplified fragments on a 6% denaturing polyacrylamide gel and

genotyping from skin samples was as described in Robertson & Gemmell (2004). Relatedness between pups of a dyad was assessed using SPAGeDi 1.0 (Spatial Pattern Analysis of Genetic Diversity; Hardy & Vekemans, 2003).

Statistical analyses

Statistical analyses were carried out in Microsoft Office Excel 2003 (Microsoft Corporation) and Minitab Release 14 (Minitab Inc.). Condition indices (mass/length) of all pups for which we had obtained morphometric data were calculated (Hall *et al*., 2001). To examine whether observed mass, condition indices and growth rates differed between pups reared by females provisioning for two pups and the remainder of pups reared by females provisioning for a single pup, one sample *t*-tests were used (Haase, 2004; Zar, 1999). Values from pups of females rearing two pups that fell outside the 95% confidence interval of the mean of all other pups were considered to be significantly different.

Nursing and attendance times of the female rearing pups X6 and X7 were compared to females rearing singleton pups, as it was expected that these may differ (Georges *et al*., 1999; Haase, 2004). The proportion of time spent nursing, in association with mother and the total times with and without mother were calculated as the proportion of observations that the pup was observed engaging in that behaviour out of the total number of observations that the pup was seen on each day. The proportion of time a mother spent ashore from the pup's perspective was also calculated using the number of days each pup was observed with their mother out of the number of days the pup was seen. These proportions were arcsine-transformed before statistical testing (Zar, 1999). Grand means for all female and male singleton pups were calculated for each

variable and one sample *t*-tests were used to test those differences in nursing and attendance times between the two pups raised by the same female and singleton pups.

Estimates of milk stealing bout rates per hour were calculated to account for occurrences that could not be observed due to the boulder profile of the colony and the difference in the number of observers throughout each season. The observed frequency of bouts was multiplied by the average proportion of marked and unmarked pups not visible for all pup counts, then dividing this result by the total number of observer hours. The proportion of total marked and unmarked pups that were visible was estimated using the proportion of marked pups visible for each count. To establish if there was a difference between the mass and condition indices of milk stealing pups versus non-milk stealing pups, a two sample *t*-test with unequal sample sizes was used. A Chi-square test investigated whether there was a significant difference between the frequencies of milk stealing attempts observed during a mother's absence period and her presence on shore.

Results

DNA Analyses

In 2003 two females were observed with two pups each. Genetic analyses found that both cases were occurrences of fostering, with one pup being the female's filial pup and other non-filial in each of the two sets (Table 1).

Table 1. Genotypic data from microsatellite DNA analyses of the two sets of potential foster pups and females. Microsatellites where no alleles were shared with the female are shown in bold. Pup 'X6' (female) did not share any alleles with the female in three genotypes, whereas pup 'X7' (male) shared alleles with the mother in all genotypes, suggesting X6 was not the female's offspring but is related to X7 (sharing alleles in 9/13=69% of genotypes). In the second case, 'Diamond' pup (male) shared alleles with the female in 11/12 genotypes, whereas the unmarked pup ('Pup 2', a male) did not share any alleles with the female in seven genotypes indicating he was a non-filial pup.

	Case 1			Case 2		
Microsatellite	Female	X6	X7	Female	Diamond	Pup 2
Hg6.1	154/154	**152/158**	152/154	154/154	-	-
HI16	155/161	155/155	155/155	141/153	141/149	**149/149**
Hg1.4	202/202	196/202	200/202	194/916	196/196	**204/204**
Lc28	144/148	**146/154**	144/144	148/152	140/148	**150/160**
Lc5	159/161	159/163	161/163	161/165	161/165	163/165
PvcA	158/162	**154/164**	152/158	158/158	158/161	**150/152**
Hg4.2	165/169	165/183	165/169	137/163	137/137	**165/171**
Pv11	155/155	155/169	155/169	155/155	155/163	**161/169**
M11a	145/181	145/149	145/177	143/145	145/159	145/179
Hg8.1	187/203	191/203	187/199	195/201	**197/211**	**185/191**
Hg6.3	236/240	236/236	236/236	234/236	234/242	236/238
Pv9	170/172	172/182	172/182	172/172	172/172	172/178
3E3	218/220	216/218	220/220	216/216	216/216	216/218

Frequency of allosuckling and fostering

During this study there were a total of 17 cases of females nursing non-filial pups over a total minimum nursing duration of three hours and twenty minutes. Thirteen were cases of milk stealing where the female was unaware of the presence of the pup (total duration of 60 minutes) and four were cases of fostering where the female was aware of the nursing pup but did not attempt to drive it away (Table 2). In 2004 the minimum frequency of allosuckling was 2.5%, or 4/159 instances of females nursing pups (out of identifiable females where their filial pup was marked).

Table 2. Instances of milk stealing, fostering and allosuckling (total number of cases of females nursing non-filial pups) in each season.

	Milk Stealing	Fostering	Allosuckling
2003 (Dec 2003 - April 2004)	11	2	13
2004 (Dec 2004 – Jan 2005)	2	2	4
Total cases	**13**	**4**	**17**

Two cases of fostering or the long-term adoption of an additional pup were observed in the 2003 season, out of a total pup estimate of 451 pups (Laura Boren, pers. comm.). This gives a minimum frequency of fostering of 0.44% per year. In the 2004 season, two cases of short-term fostering (fostering occurring on one occasion) involving two identifiable pups (3% of all known pups) were observed. No females were observed adopting additional pups during this season. The frequency of fostering was 1.3% or 2/159 observations of identifiable females nursing marked pups. A comparison between years was not possible because of the different circumstances of the fostering events.

Fostering: long-term events (adoptions)

Adoption Case 1

Two pups were observed together with a female on six occasions between 8 December 2003 and 27 April 2004 (Figure 1). The female was not identifiable and only one of the pups was marked on 30 January 2004. Before this date it was assumed that these were the same individuals as they were always in the same location and because adoption is rare it was considered unlikely that there would be more than one occurrence in the same small area. The adoption was first observed on 8 December 2003, when two pups were observed resting next to a female; one in contact with the female and the other within one metre away. The female looked at both pups and made naso-nasal contact with the closest pup with no rejection of either pup. The pups were probably no more than two weeks old judging by their size and the fact that the first born pup in this sector were observed late November. The next day the same situation was observed in the same location. On 16 December 2003 they were observed again when both pups took turns at nursing. The pair were not seen again until 29 January when both pups were observed nursing on and off for one hour and ten minutes. The female looked at both pups and made naso-nasal contact with each occasionally. They were observed together only twice more. On 30 January one pup (filial pup, 'Diamond') was caught, measured, marked and skin-sampled and a hair sample was obtained from the female. The other pup was skin-sampled on 27 April. Pup 'Diamond' was seen alone with a female occasionally, presumably his mother but the female was not identifiable.

Figure 1. Fostering: female nursing her filial pup (‘Diamond’, on right) and non-filial pup (left) simultaneously on 27 April 2004. Photo by Abigail Caudron.

The filial and non-filial pup (both males) appeared a similar weight and condition on all observations except on 27 April 2004 when the non-filial pup appeared to be in a relatively poor condition (Figure 1). From morphometric data obtained for the filial pup 'Diamond', it was found that his mass and condition were significantly greater than that of other male pups on 30 January, but on 26 March his mass and condition were significantly less than that of other male pups (Table 3). His growth rate between January and March was significantly less than that of other male pups (Table 3).

Table 3. Mass, condition indices and growth rate (between 30 January and 26 March) from two captures of the filial pup 'Diamond' (a male) as compared with those (given as the confidence interval of the mean) for singleton male pups (*t* values and significance (*P*) established at 95% confidence interval).

	Filial pup	Males	*t*	*P*	n
Mass (kg)					
30 Jan	9.8	8.98 ± 0.46	-3.62	**0.001**	42
26 March	10.6	11.7 ± 0.53	4.04	**<0.001**	48
Condition (kg cm^{-1})					
30 Jan	0.1307	0.1185 ± 0.0048	-5.15	**<0.001**	42
26 March	0.1342	0.1399 ± 0.0056	2.06	**0.045**	48
Growth rate (g/day)	14.3	55.5 ± 9.2	9.05	**<0.001**	39

Adoption Case 2

The second case of a female with two pups was discovered on 22 December 2003. Both pups were estimated at one day old or less, with placentas attached. The previous day a pup was observed soon after birth (<1 hour old) in the same location as the two pups were found. This was on the edge of a rocky island, an unusual location to give birth so it was assumed it was one of the pups. The second pup was probably born nearby the same day or the next morning. The pups were observed nursing at the same time on numerous occasions (Figure 2). The male pup (numbered X7) was successful in excluding the female foster pup (numbered X6), a smaller pup, from access to a teat on many occasions.

a

b

Figure 2. Female with two pups X6 and X7 a) with the female on 11 February 2004 (7 weeks old): X6 (foster pup) on the left, X7 (filial pup) on the right, nursing b) nursing off the female simultaneously at just over 5 months old on 27 May 2004 (this photo by Laura Boren).

The female pup X6 was significantly lower for both mass and condition at birth and throughout the year than all other female pups (Table 4). The male pup X7 was not significantly different in mass or condition at birth but from January to October he was of a lower mass and poorer condition than all other single male pups (Table 4). X6 had a significantly lower rate of growth from both birth to March and March to October (Table 5). X7 had a significantly lower rate of growth from birth to March but he was not different from all other pups from March to October (Table 5). X6 spent a significantly lower proportion of time nursing and with and without her foster mother than singleton pups (Table 6). Time spent nursing and with and without mother did not differ between X7 and singleton pups (Table 6). The proportion of days the mother spent ashore from the pups' perspective (proportion of days where female and pup were observed in association) was significantly lower for X6 than female singleton pups, but there was no significant difference between X7 and male singleton pups (Table 6).

Table 4. Mass and condition indices from captures of pups X6 (female) and X7 (male) reared by one female as compared with those (given as the confidence interval of the mean) for singleton female and male pups, respectively, of the same age (*t* values and significance (*P*) established at 95% confidence interval).

Pup	Pup age/date	Pup mass (kg)	Singleton pup mass (kg)	*t*	*P*	Pup condition (kg cm^{-1})	Mean condition of singletons (kg cm^{-1})	*t*	*P*	n
X6	Birth (0-5 days)	3.3	4.6 ± 0.24	10.89	**<0.001**	0.065	0.076 ± 0.003	6.91	**<0.001**	51
	Jan (32-46 days)	4.8	7.5 ± 0.27	19.66	**<0.001**	0.074	0.107 ± 0.003	20.49	**<0.001**	62
	March (86-119 days)	6.3	10.9 ± 0.54	17.16	**<0.001**	0.091	0.134 ± 0.006	15.53	**<0.001**	33
	Oct (294-313 days)	6.4	11.5 ± 1.61	6.80	**<0.001**	0.089	0.134 ± 0.016	6.08	**<0.001**	14
X7	Birth (0-5 days)	4.6	4.8 ± 0.26	1.75	0.087	0.077	0.078 ± 0.003	0.74	0.466	53
	Jan (32-46 days)	5.8	8.3 ± 0.28	17.81	**<0.001**	0.076	0.113 ± 0.003	22.94	**<0.001**	82
	March (86-119 days)	7.8	11.7 ± 0.51	15.54	**<0.001**	0.101	0.141 ± 0.005	14.62	**<0.001**	47
	Oct (294-119 days)	8.8	13.17 ± 0.88	10.11	**<0.001**	0.106	0.149 ± 0.009	9.71	**<0.001**	36

Table 5. Comparison of growth rates between the pups X6 (female) and X7 (male) reared by one female and the mean for all other singleton female and male pups, respectively (*t* values and significance (*P*) established at 95% confidence interval). *n* represents the number of singleton pups for which growth rate was obtained. *Female and male growth rates were pooled for March-October because there was no difference among genders (*t*-test: *t*=-0.25, df=6, *P*=0.41).

Pup ID	Period	Pup growth rate g/day	Singleton pup growth rate g/day	*t*	*P*	n
X6	Birth-March	31.58	57.89 ± 4.97	11.02	**<0.001**	22
	March-Oct*	0.5	11.62 ± 7.17	3.51	**0.007**	10
X7	Birth-March	33.68	65.95 ± 5.76	11.46	**<0.001**	30
	March-Oct*	5.03	11.62 ± 7.17	2.08	0.067	10

Table 6. Nursing and attendance time proportions from the pups' perspective for the pups X6 and X7 raised by one female as compared with those (given as the confidence interval of the mean) for singleton pups (*t* values and significance (*P*) established at 95% confidence interval). Female and male pups were pooled (n=42) for all variables except the females' proportion of time in attendance because they were significantly different (*t* test: t=1.86, df=36, *P*=0.04).

Pup ID	Variable	Pup mean proportion	Singleton mean proportion	*t*	*P*
X6	Nursing	0.086	0.107 ± 0.038	3.55	**0.001**
	Non-nursing association with female	0.089	0.120 ± 0.044	4.55	**<0.001**
	Total time with female	0.175	0.227 ± 0.071	4.75	**<0.001**
	Pup without female	0.870	0.776 ± 0.071	-5.86	**<0.001**
	Females' proportion time in attendance	0.316	0.479 ± 0.096	7.01	**<0.001**
X7	Nursing	0.111	0.107 ± 0.038	-0.79	0.434
	Non-nursing association with female	0.111	0.120 ± 0.044	1.36	0.180
	Total time with female	0.221	0.227 ± 0.071	0.41	0.682
	Pup without female	0.778	0.776 ± 0.071	-0.22	0.829
	Females' proportion time in attendance	0.420	0.420 ± 0.102	-0.01	0.993

The filial pup X7 unsuccessfully attempted to nurse off his mother numerous times after his last successful nursing bout on 28 November (Figure 3). The pup was often observed displaying milk thieving behaviour, keeping a low profile and approaching slowly. His mother was tolerant of him until he attempted to nurse, when she would reject him with open-mouth threats.

a  b 

Figure 3. Pup X7 attempting to nurse off his mother in December 2004 (12 months old) a) on 12 December; pup is emaciated b) displaying milk stealing behaviour (low profile, moving in slowly).

X7 was last observed nursing from his mother on 28 November 2004, when he was just over 11 months old. X6 was never observed nursing from her foster mother in the 2004 field season. She was nursing on 11 October 2004 when we captured her and obtained measurements. However, X7 remained in the colony until 17 December 2004 and X6 until 11 January 2005. They were the last yearlings to remain in the colony with the exception of one pup whose mother abandoned her newborn on the day of birth and continued to nurse her yearling that was in a poor condition. When last observed in the colony, X7 was emaciated (Figure 3a) and X6 appeared in a better, but poor, condition. It was unsure whether they would have survived but neither was found dead during daily surveys until 28 January 2005.

Fostering: short-term events

In the 2004 field season there were two one-off fostering events. The first one occurred on 17 December 2004 and involved the fostered pup X6 from the previous season (361 days old), who was observed nursing from an identifiable female for one hour and 31 minutes. This female was in labour, and she was seen with a newborn the following day. The foster mother of X6 had already given birth to her newborn and had ceased nursing X6 and X7. The last time X6's measurements were obtained, in October, she was of significantly lower mass and condition than other female pups measured at the same time (mass: t=6.80, n=14, P<0.001; condition: t=6.08, n=14, P<0.001; Table 4).

The second occurrence of short-term fostering occurred on 15 January 2005 with a known female nursing a marked non-filial pup. Nursing occurred for a minimum of 10 minutes. The female and her pup had been followed in the previous season and this season her pup was also marked. Her pup was identified at least five metres away while the fostering event took place. The female was resting but alert, and a few times sniffed the non-filial pup but went back to resting without making any attempt to drive her away. The fostered pup (female) had a significantly greater mass (8.3 kg) and condition (0.1153 kg cm^{-1}) compared with other female pups measured at the same time (one-sample t-test, mass: t=-3.68, n=21, P=0.001; condition: t=-3.02, n=21, P=0.007). In the previous season, this foster mother was captured and measurements obtained. She had the smallest mass (32.4 kg) out of nineteen females caught ($\bar{X}$ = 40.3 kg, range 32.4 - 51.7 kg) which suggests she may be young and maternally inexperienced.

Milk stealing

In the 2003 and 2004 field seasons, 84 and 19 milk stealing attempts were documented, respectively. In 2003, 13 (7.6% of 170) marked pups were involved in milk stealing attempts. In 2004, 8 (12.9% of 62) marked pups were observed making attempts at milk stealing. In 2004, all except one occurrence of milk stealing occurred in January. During January the rate of milk stealing attempts observed was less than one case per day (0.9 cases/day, n=21 days).

The earliest milk stealing attempts observed were by pups two weeks old, which occurred in mid-December in both years. Estimates of milk stealing bout rate in the first season increased from December 2003 to March 2004, but decreased in April 2004 (Figure 4). A similar increasing trend from December to January was observed in the second season. The rate of milk stealing bouts was higher in January 2005 than January 2004 (Figure 4). December rates were not comparable between years because there were few occurrences of milk stealing.

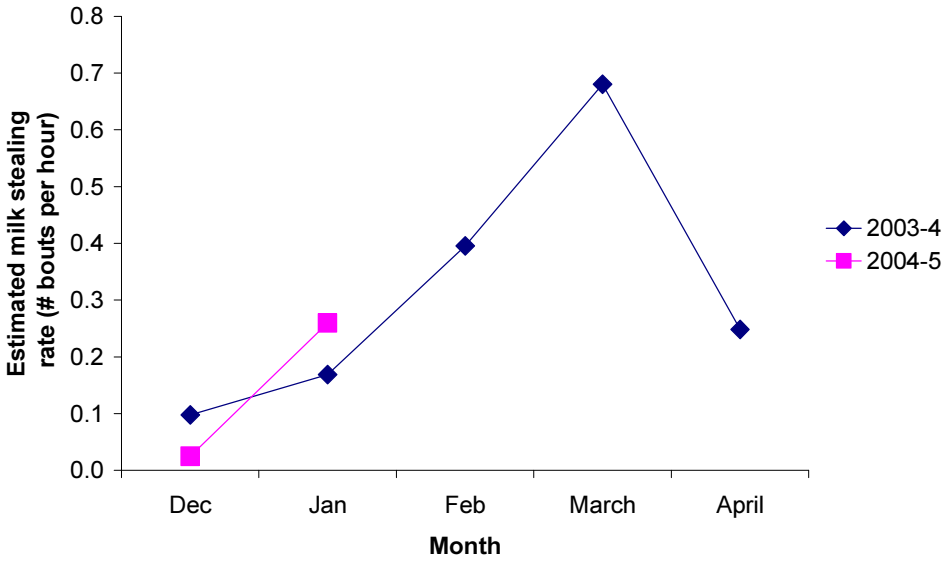


Figure 4. Estimated rates of milk stealing bouts for each month and season. Rates took into account the proportion of pups not visible for each pup count and the number of observer hours. Observations did not occur from February to April 2005.

Many milk stealing attempts were facilitated by a thieving behaviour exhibited by pups (Figure 5). They would quietly approach the exposed belly of the female from the side or from behind the female. Many would pause and lie down with fore flippers at right angles to the body for a few seconds then get up and move closer, sometimes repeating this behaviour a few times from about one metre away until they had reached the female's belly. However, some attempts appeared to be opportunistic; pups would be walking past a sleeping female and after noticing the exposed belly, approach and nose the female. Pups were also observed attempting to nurse from territorial bulls and other pups. The observed success rates of milk stealing attempts were 13% and 11% in the 2003 and 2004 seasons, respectively. Twelve females and nine male pups were observed making attempts at milk stealing (both seasons). The total duration of successful milk stealing bouts was 3600 seconds (60 minutes) and the average was 302 seconds (range 5-1200 seconds, n=12). During milk stealing attempt bouts, pups often made several attempts at milk stealing from one or more females. There were a total of 216 attempts on 126 females plus 4 bulls and 3 pups. The mean number of attempts per bout was 2.2 (range 1-27, n=98) and the mean number of individuals that pups attempted to milk steal from per bout was 1.3 (range 1-7, n=98). Forty-two percent of females were in association with their filial pup when pups attempted to milk steal. Where the reaction of the female was recorded (n=177), the proportions of each reaction are as follows: open-mouth threat 56%, female moved and the stealer left 15%, the female's filial pup chased the stealer away 7%, female and her filial pup chased the stealer away 6%, female growl 4%, pup left on own accord 4%, female lunge 3%, female bit stealer 3%, female sniffed or made naso-nasal contact with the stealer but did not threaten pup 2%.

a b

c d

e

Figure 5. Milk stealing attempt bout by pup #103 (4 months old) on 9 April 2004 a) pup sneaks up to a sleeping female b) female wakes up, pup moves away c) looks for a teat on a sleeping pup d) attempts to nurse from a territorial bull e) milk stealing success: pup finds a sleeping female. Photos by Abigail Caudron.

Masses and condition indices were not significantly different between pups making attempts at milk stealing (milk stealers) than pups not observed attempting milk stealing (non-milk stealers) in either year (Table 7). However, when each milk stealer was investigated individually, it was found that 5 and 6 out of 13 known pups fell below the 95% confidence interval for the mean of non-milk stealers of the same gender, for mass (Figure 6) and condition (Figure 7), respectively, in 2003. In 2004, one milk stealer (out of 8) fell outside the confidence interval of non-milk stealers for mass (Figure 8) and one milk stealer for condition (Figure 9). For both years, the condition of 7 known pups (33.3% of milk stealers, n=21) fell below the confidence interval of the mean for the non-milk stealer pups measured at the same time and of the same gender. The three pups with the greatest number of milk stealing attempt bouts observed (pups X6, 103, 86 with 11, 9 and 4 attempts, respectively) were three of the five pups whose mass and condition were significantly lower than non-milk stealers in 2003 (Figure 6, 7).

Milk stealing attempts by known pups were more prevalent when their mothers were not present in the colony (73% of attempts, $\chi^2 = 0.09$, n=44, $P = 0.005$). Milk stealing attempts were observed between 1-8 days since the mother's departure, with 41% (n=32) of attempts occurring 2 days after departure. The mean foraging trip length was 2.7 days (range <1-14) in 2003 and 4.2 days (range <1-15) in 2004 (Laura Boren, pers. comm.).

Table 7. Mean mass and condition indices of milk stealers compared with those of non-milk stealers for each gender in each year (*t*-tests: values given as $\bar{X} \pm$ SD).

		Milk Stealers $\bar{X}$	Non-milk stealers $\bar{X}$	*t*	*P*
2003					
Females	Mass (kg)	10.2 ± 2.93	10.8 ± 1.46	-0.49	0.65
	Condition (kg cm^{-1})	0.1285 ± 0.0305	0.1340 ± 0.0148	-0.40	0.71
Males	Mass (kg)	11.85 ± 1.70	11.64 ± 1.84	0.24	0.82
	Condition (kg cm^{-1})	0.1391 ± 0.0173	0.1399 ± 0.0195	-0.09	0.93
2004					
Females	Mass (kg)	7.6 ± 0.63	7.4 ± 1.37	0.44	0.67
	Condition (kg cm^{-1})	0.1134 ± 0.0086	0.1067 ± 0.0119	1.30	0.24
Males	Mass (kg)	8.2 ± 0.43	8.6 ± 1.23	-1.27	0.22
	Condition (kg cm^{-1})	0.1160 ± 0.0026	0.1188 ± 0.0122	-1.01	0.32

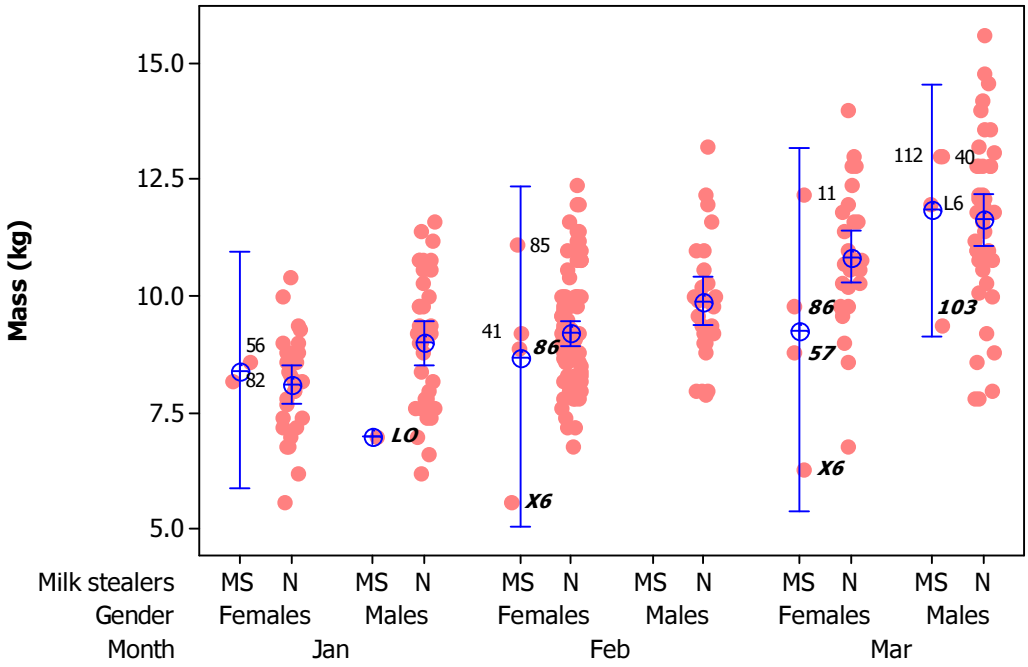


Figure 6. Mass of milk stealers (MS) compared with that of non-milk stealers (N) in 2003. Individual values are plotted as well as means and 95% confidence interval bars, with milk stealers labelled with their identification number or name. Values of milk stealers that fall below the confidence interval of non-milk stealers are italicised and in bold.

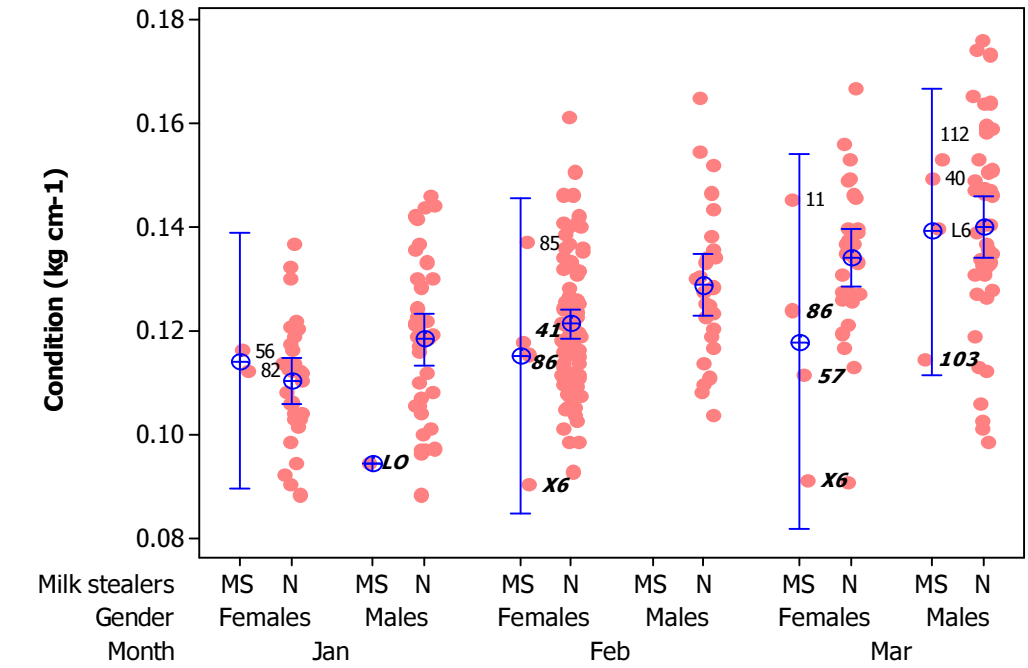


Figure 7. Condition of milk stealers (MS) compared with that of non-milk stealers (N) in 2003. Individual values are plotted as well as means and 95% confidence interval bars, with milk stealers labelled with their identification number or name. Values of milk stealers that fall below the confidence interval of non-milk stealers are italicised and in bold.

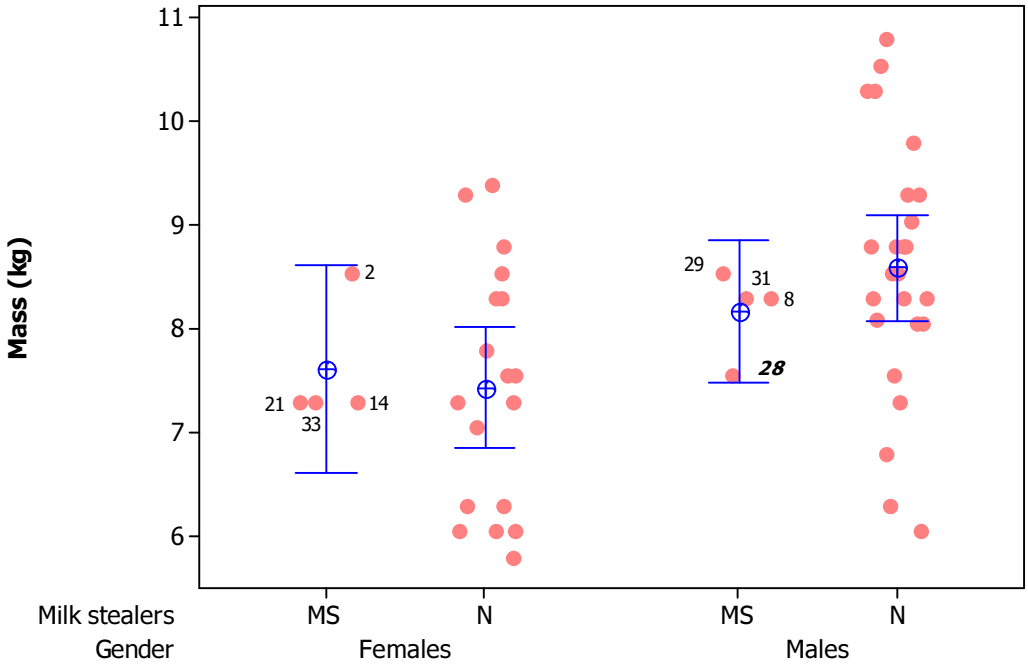


Figure 8. Mass of milk stealers (MS) compared with that of non-milk stealers (N) in 2004. Individual values are plotted as well as means and 95% confidence interval bars, with milk stealers labelled with their identification number or name. Values of milk stealers that fall below the confidence interval of non-milk stealers are italicised and in bold.

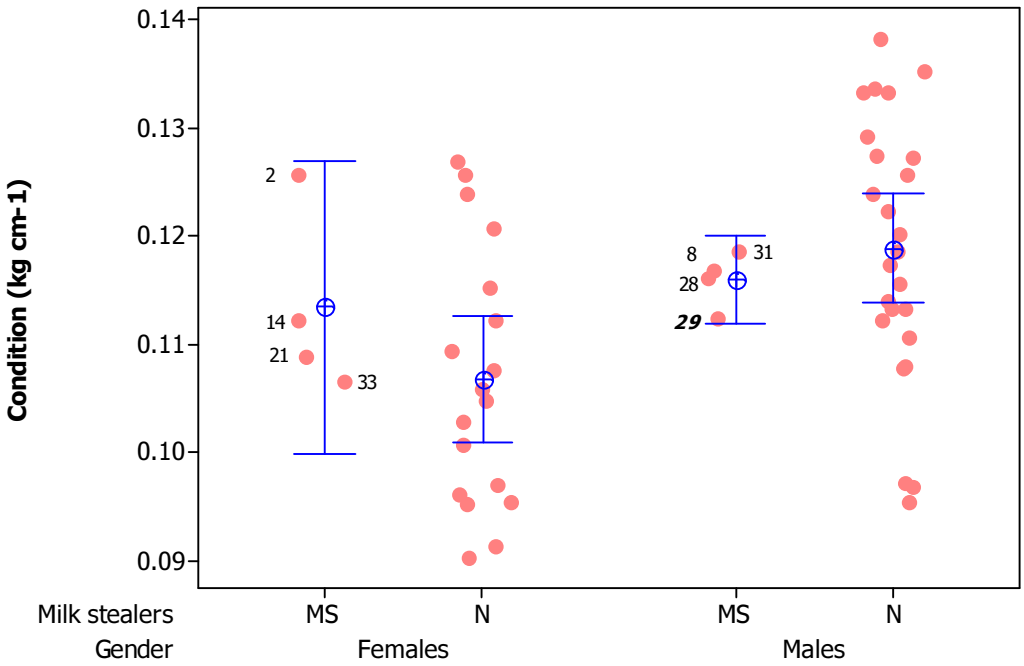


Figure 9. Condition of milk stealers (MS) compared with that of non-milk stealers (N) in 2004. Individual values are plotted as well as means and 95% confidence interval bars, with milk stealers labelled with their identification number or name. Values of milk stealers that fall below the confidence interval of non-milk stealers are italicised and in bold.

Incidence of fostering in pinnipeds

I sought information on incidences on fostering in pinnipeds via an email contact list of marine mammal researchers. The focus was on fostering in otariids; however, some accounts in phocids have been included for comparison of frequencies. Numerous unpublished cases of fostering were revealed (Table 8). Fostering or potential fostering cases have been listed for 7 species of phocids and 9 species of otariids in this review; however the list is not exhaustive. Some observations of aware (i.e. not milk stealing) females nursing two pups were not confirmed cases of fostering, but they have been included here because of the even greater rarity of twinning (Spotte, 1982). Many observations were singular, but where frequency was known, fostering occurred in proportions from 0.3-90% in phocids and 0.17-11% in otariids. Over 80 cases in otariids have been reported.

Table 8. Review of fostering in pinnipeds. Common names are listed with species names underneath.

Species	Location	Date	Behaviour	Number of cases/frequency (%)	Sources
Phocids					
Northern elephant seal *Mirounga angustirostris*	Año Nuevo Island, California	1967	Pups nursing from more than one female	Unknown	Fogden, 1968
	Año Nuevo Island, California	1968-71	Females rearing two pups; females adopting pups after losing their own	2; 5	Le Boeuf *et al*., 1972
	Año Nuevo Island, California	1976-7	Pups nursing from two females each	6	Reiter, 1978
	Año Nuevo Island, California	1976-80	Females adopting orphan pups	98	Riedman & Le Boeuf, 1982
Southern elephant seal *M. leonina*	Macquarie Island	1965	Female nursing a pup separated from his own mother	1	Bryden, 1966
	South Georgia, Southern Ocean	1988-1990	Females rearing two pups	3 (0.3%)	Arnbom *et al*., 1997
	Marion Island, South African subantarctic	1980's	Female nursing non-filial pup	1 (0.73%)	Wilkinson, 1992
	Peninsula Valdés, Chubut, Argentina	2002	Female rearing two pups	1	M. Briga, pers. comm.
Grey seal	Orkney Islands, Scotland	1966	Females nursing two pups	2	Fogden, 1968
Halichoerus grypus	Orkney Islands, Scotland	1967	Females nursing more than one different pup	10	Fogden, 1971
	Hebrides and Orkney Islands, Scotland	1963-66	Pups nursing from more than one female	Unknown	Smith, 1968
	North Rona, Scotland	1986-89	DNA analyses found unrelated mother-pup pairs	6 (6%)	Amos *et al*., 1993

Table 8. Review of fostering in pinnipeds (continued).

Species	Location	Date	Behaviour	Number of cases/frequency (%)	Sources
Grey seal *Halichoerus grypus*	Sable Island, Canada; Orkney Islands; Ramsey Island, Wales	1993-4	Females nursing non-filial pups and DNA analyses	3-28%	Perry *et al*., 1998
	Isle of May, Scotland	1997	Females nursing non-filial pups	17	McCulloch *et al*., 1999
Spotted seal *Phoca largha*	North and East of Pribilof Islands, Alaska	1971	Female accepting a non-filial pup after the filial pup was taken from her	1	Burns *et al*., 1972
Harbour seal	Sable Island, Canada	1990	Females nursing non-filial pups	8 (10%)	Boness *et al*., 1992
P. vitulina	Sable Island, Canada	1991-6	DNA analyses and behavioural data find females nursing non-filial pups	4.6-14.4%	Schaeff *et al*., 1999
Hawaiian monk seal *Monachus schauinslandi*	Laysan Island and East Island (French Frigate Shoals), Hawaii	1987-89	Females nursing non-filial pups	9 (53%), 9-26 (87-90%)	Boness *et al*., 1998 Boness, 1990
Weddell seal *Leptonychotes weddellii*	McMurdo Sound, Antarctica	1966-70	Females nursing non-filial pups	14 (7.8%)	Stirling, 1975
	McMurdo Sound, Antarctica	1996-8	Females nursing two pups; DNA analyses	4	Gelatt *et al*., 2001
Otariids					
Stellar sea lion *Eumetopias jubatus*	Timbered Island, Alaska	1996	Female nursing a non-filial pup with her own on one occasion	1	Porter & Trites, 2004
	Chiswell Island, Alaska	2003	Female adopting a non-filial pup after losing her own	1	Harris *et al*., 2005

Table 8. Review of fostering in pinnipeds (continued).

Species	Location	Date	Behaviour	Number of cases/frequency (%)	Sources
Galapagos sea lion *Zalophus californianus wollebaeki*	Galapágos Islands	1976-9	Female nursing two pups	few	Trillmich, 1981
	Galapágos Islands	1971-2001	Females nursing two pups	4-8	D. Day, pers. comm.
Australian sea lion *Neophoca cinerea*	Dangerous Reef, Australia	1970	Abduction by females who had lost their own pups	3	Marlow, 1972
New Zealand sea lion *Phocarctos hookeri*	Enderby Island, Auckland Islands, New Zealand	1975	Female nursing two pups	1	Marlow, 1975
	Enderby Island, Auckland Islands, New Zealand	1995-7	Females nursing more than one pup	6%	Childerhouse & Gales, 2001
South American fur seal *Arctocephalus australis*	Galapágos Islands	1976-9	Female nursing two pups	1	Trillmich, 1981
	Punta Coles, Ilo, Peru	2000	Female nursing two pups	1	M. Stevens, pers. comm.
Cape fur seal *A. pusillus pusillus*	Sinclairs Island, Seal Island, South Africa	1947-8	Females swapping pups during disturbance soon after birth	Unknown	Rand, 1955, G. Hofmeyr, pers. comm.
Subantarctic fur seal *A. tropicalis*	Marion Island, Indian Ocean	1981	Female rearing two pups to weaning	1	Bester & Kerley, 1983
	Amsterdam Island, Indian Ocean	1995	Female rearing a non-filial pup with her filial pup	1	Georges *et al*., 1999
	Amsterdam Island, Indian Ocean	1999-2000	Females nursing a non-filial pup	5	G. Beauplet, pers. comm.
	Amsterdam Island, Indian Ocean	2000	Female nursing two pups	1	I. Charrier, pers. comm.

Table 8. Review of fostering in pinnipeds (continued).

Species	Location	Date	Behaviour	Number of cases/frequency (%)	Sources
Antarctic fur seal	Schlieper Bay, South Georgia	1979-81	Females nursing two pups	2	Doidge, 1987
A. gazella	Bird Island, South Georgia	1989-90	Females nursing non-filial pups	34	Lunn, 1992
	Bird Island, South Georgia	1994-6	DNA analyses found unrelated mother-pup pairs	21 (11%)	Gemmell, 2003
	Bird Island, South Georgia	1990-1993	Females nursing two pups; females nursing pups after having lost their own	several	J. P. Y. Arnould, pers. comm.
New Zealand fur seal	Otago Peninsula, NZ	1987	Female nursing two pups	1	Armstrong, 1988
A. forsteri	Kangaroo Island, South Australia	1992	Female nursing two pups	1	S. Goldsworthy, pers. comm.
	Kangaroo Island, South Australia	2001-3	Females rearing additional non-filial pup	3 (0.17%)	Haase, 2004
	Otago Peninsula, NZ	1998	Female suckling her mother's pup	1	S. McConkey, pers. comm.
	Ohau Point, Kaikoura, NZ	2002-5	Female rearing additional non-filial pup (confirmed by DNA analyses), females nursing non-filial pups	4 (0.44-1.3%)	This study

Discussion

Frequencies of allosuckling in pinnipeds

At Ohau Point allosuckling in the form of both fostering and milk stealing was observed. Until recently, both of these behaviours were thought to be nonexistent or extremely rare in otariids (Marlow, 1972; Stirling, 1975) but this study provides further evidence to the contrary. Fostering has been observed in most species of otariids but generally occurs at lower frequencies than those observed in phocid species (Table 8). The frequencies of fostering found in this study (0.44-1.3%) is similar to the 0.17% frequency found in a study of New Zealand fur seals (*Arctocephalus forsteri*) in Australia (Haase, 2004). The fostering frequencies in this species are considerably lower than those found in Antarctic fur seals, *A. gazella* (11%; Gemmell, 2003) and New Zealand sea lions, *Phocarctos hookeri* (6%; Childerhouse & Gales, 2001). Infrequent occurrences of fostering have also been noted in the subantarctic fur seal (*A. tropicalis*), Galapágos sea lion (*Zalophus californianus wollebaeki*), South American fur seal (*A. australis*), Australian sea lion (*Neophoca cinerea*), Cape fur seal (*A. pusillus pusillus*) and the Stellar sea lion (*Eumetopias jubatus*). Many of these reports were observations of females nursing two pups without rejection and they have been assumed to be fostering because of the assumption that twinning is extremely rare (Childerhouse & Gales, 2001; Spotte, 1982). However we cannot exclude the possibility that some of these cases were incidences of twins.

Potential costs of provisioning to two pups

Adopting a second pup costs the filial pup, because provisions are directed to foster pups instead of filial pups. In the first adoption case, the filial pup was of a significantly lower mass and condition and exhibited a lower growth rate than other singleton male pups, later in the season (Table 3). Morphometry data was not obtained for the foster pup, but he appeared in a worse condition than the filial pup.

Similarly, mass and condition of both the filial pup X7 and the foster pup X6 were significantly lower than all other singleton pups of the same sex throughout the year (Table 4). Growth rates of both pups were significantly lower than singleton pups from birth to March, but from March to October X7's growth rate was not significantly lower than the mean for singleton pups (Table 5). However, he appeared to lose weight between October and December when he was of a very poor condition, even more so than X6. Lower pup growth rates (Doidge, 1987) and weaning weights (Doidge, 1987; Georges *et al*., 1999) were also observed in other studies of otariid females rearing two pups. Lower body conditions were observed in *A. forsteri* pups raised by a mother provisioning for two by Haase (2004). Conversely, Bester & Kerley (1983) found no difference in weaning mass between singletons and two pups raised by one female in *A. tropicalis*.

The foster female spent the same amount of time with her offspring X7 but less time with her adopted pup X6 than other mother-singleton pup pairs (Table 6). This suggests the female did not alter her foraging cycle to compensate for rearing two pups. Haase (2004) found that *A. forsteri* foster mothers made shorter foraging trips and longer attendance bouts compared to single-pup mothers. However, in this study

the foster mother may have made more overnight foraging trips than mothers of singleton pups, but this data could not be obtained. The close proximity of the colony to the continental shelf feeding grounds (Carey, 1992) could have allowed the female to gain additional food during extra overnight foraging trips. She was probably unable to provision the same amount of milk to each pup as other females provisioning to one, however she nursed her filial pup X7 for a longer duration, possibly to compensate for his lack of nutrition. This is consistent with a study by Georges *et al.* (1999) that found that the biological pup of reared with an adopted pup by the same female weaned later. X7 survived to weaning, however, both pups were last seen in the colony in poor condition so their probability of surviving to breeding was probably low (Hall *et al*., 2001). We would also expect the male filial pup X7 to exhibit a reduced reproductive success, should he survive to breeding age, because a small body size would disadvantage him in competing for territories (Bonner, 1984). The risk of reducing the filial pup's probability of survival and the female's reproductive success should select against fostering behaviour (Riedman, 1982).

Fostering theory

The first foster mother and two pups were first observed when the pups were up to two weeks old, which suggests it may have occurred before recognition was fully developed between mother and pup, possibly caused by a disturbance in the colony. A female was observed in another area retrieving a young non-filial pup during a disturbance by humans. Disturbance caused by females fighting over space resulted in a pup swap for over one hour and disturbance has been considered a major contributor to fostering behaviour in some studies (Rand, 1955; Fogden, 1968; Stirling, 1975). Therefore, we cannot rule out the possibility that our disturbance in the colony while

marking pups resulted in a female bonding with two pups. Density may have also been a factor (Fogden, 1968; Riedman & Le Boeuf, 1982), as the pup-swapping case described above occurred when there appeared to be a higher density of females and newborns than in the previous season (pers. obs.), however no density estimates were obtained for the area where the adoption occurred. A lack of maternal experience may have been a factor (Riedman, 1982; Boness *et al*., 1992; Roulin, 2002). The age of the female was not known but the fostering case occurred in a sector that was occupied by breeding females only since the 2002-2003 season (L. Boren, pers. comm.) and younger females tend to colonise new pupping areas (Goldsworthy & Shaughnessy, 1994).

In the second case of long-term fostering, the adopted pup X6 shared alleles with the filial pup, X7, in 9/13 (69%) genotypes (Table 1). This high relatedness between the pups suggests that they shared the same father. They were born in the same area and since females were often highly site-specific (pers. obs.), they were probably conceived in the same territory by the same bull. X6 also shared alleles with her foster mother in 10/13 (77%) of genotypes, suggesting the pup's birth mother may have been a daughter or mother of the fostering female. This has implications for the potential cause of fostering, as the foster female may have increased her inclusive fitness by nursing the offspring of a relative, as suggested through kin selection theory (Hamilton, 1964). Gemmell (2003) found that Antarctic fur seal (*Arctocephalus gazella*) relatedness was higher for foster mother-pup pairs than that observed for the total population, suggesting that kin selection played a role in fostering. The observation of a female *A. forsteri* nursing her mother's pup on Otago Peninsula (S. McConkey, pers. comm.), appears to support this theory, however the colony was

established by one female so all females are related. In kin selection theory, relatives must be chosen preferentially for fostering (Hamilton, 1964).

The female fostering X6 may have jeopardised the survival and breeding potential of her filial pup which may reduce her reproductive success, suggesting that the costs of fostering would outweigh the benefits of increased inclusive fitness. Since that X6 and X7 were born around the same time and likely close together, and they were first observed with the female the day after the birth of one, it seems likely that the female developed a mother-pup recognition bond with both pups. Colony disturbances may have resulted in X6 ending up near the female, who learned to recognise the non-filial pup as well as her offspring. Observations of females fighting over pups of a few days old (see Chapter 2) and cases in other species of females swapping pups suggest that high densities, female aggression and disturbances could cause erroneous development of recognition of non-filial pups and subsequently long-term adoption (Rand, 1955; G. Hofmeyr pers. comm.). The high relatedness of X6 and X7 may have also affected the ability of the female to distinguish between the pups, especially if the female was maternally inexperienced as these females are more likely to make recognition errors (Lunn, 1992; Boness *et al*., 1992; Harris *et al*., 2005).

Fostering by pinniped females while giving birth has previously been observed (McCulloch *et al*., 1999). In that study a female grey seal (*Halichoerus grypus*) abandoned her newborn and left with the non-filial pup (McCulloch *et al*., 1999). However, in our observations of a female fostering while in labour, the foster mother was never again observed nursing the non-filial pup but was observed with her newborn on several occasions. It is possible that this female was distracted by being in

labour, as she was alert but did not sniff the non-filial pup. The pup was X6, also fostered by the mother of X7, who was in extremely poor condition and was the pup observed making the most milk stealing attempts in the previous season. The foster female may have been X6's birth mother, but it seems unlikely that X6 was nursed by two females given her poor condition and low growth rate throughout the season, and X6 had never been observed nursing from this female previously. She may have been attempting to milk steal as she was in poor condition and the female did not reject her because she was distracted with being in labour.

In the third case of fostering the foster mother was still provisioning to her filial pup. The propensity of *A. forsteri* females to return to give birth at their natal colony (Stirling, 1971b) and the recent recolonisation of the Ohau Point colony (Boren, 2001) suggest that relatedness among females may be high. Therefore, the hypothesis relating kin selection to fostering cannot be ruled out. This case of fostering is probably more likely to be a result of misdirected parental care by a young female of limited maternal experience, given her small size. Young females may be more likely to make recognition errors (Lunn, 1992). This is consistent with studies that found foster mothers were most commonly young females (Boness *et al*., 1992; Lunn, 1992; Harris *et al*., 2005).

Frequency and basis for milk stealing

Milk stealing by pups is a relatively common behaviour as compared with fostering. The success rate of 11-13% and the total duration of milk stealing successes being only 3600 seconds (average 302 seconds per bout) suggest that the costs to females are low. It is beneficial for nutritionally stressed pups to steal milk, either when they

are in a poor condition or when their mother is away on a foraging trip. Despite Ohau Point females' foraging trips often being short, pups would still attempt to steal milk. The foster pup X6 was in a poorer condition than most other marked pups and was the pup observed making the most attempts at milk stealing. It is possible that milk stealing may have improved her condition, as X7 was never observed to milk steal and he was in a worse condition in the following season (pers. obs.). The general trend of milk stealing was that the rate increased as the season progressed (Figure 4), suggesting the behaviour may be linked to the increasing length of foraging trips over time during lactation (Trillmich, 1990; Boness & Bowen, 1996) because longer maternal absence periods probably result in more pups being nutritionally stressed (Charrier *et al*. 2002a). By comparing the rates between January 2004 and January 2005, it appears that milk stealing bouts were more frequent in the second season (Figure 4). The second season was an El Niño season, which may have resulted in a January 2005 rate one and a half times higher than that of 2004 because of an increase in nutritional stress of pups. Foraging trip duration was also longer in the second season (2004: $\bar{X} = 2.7$; 2005: $\bar{X} = 4.3$ days; L. Boren, pers. comm.), likely because extreme environmental conditions affect prey and females' ability to forage successfully (Trillmich, 1990). This data supports the results from other studies that found increases in aberrant behaviours such as milk stealing under extreme environmental conditions during El Niño years (Ono *et al*., 1987; Ono & Boness, 1991; Lunn, 1992; Soto *et al*., 2004).

Milk stealing did not appear to be more common in males than females, which is inconsistent with the findings of Reiter (1978). In that study it was concluded that milk stealing is a strategy to enhance fitness since an advantage in size in males is of a

great importance in polygynous animals. It was also found that canine teeth of males erupted later which allowed a greater success rate and therefore greater advantages for male pups (Reiter, 1978). In *A. forsteri* it appears that gaining supplementary nutrition by milk stealing is important for any nutritionally stressed pups of either gender. The benefits of milk stealing appear to outweigh the costs in this species, since the most common reaction of females to milk stealers was an open mouth threat. Females bit the non-filial pup in only 3% of milk stealing attempts and no pups were injured during attempts. The danger may be present though, as necropsy of one pup revealed head and neck trauma and a bite wound possibly from an adult female (L. Boren, pers. comm.). This contradicts observations in other species of frequent bites or injuries inflicted on non-filial pups by females (Reiter, 1978; Roux, 1986; Ono *et al*., 1987; Porter & Trites, 2004; Soto *et al*., 2004; Harris *et al*., 2005). I suggest that a lower cost of milk stealing to pups does not select against this behaviour as strongly as in other species, therefore milk stealing behaviour is relatively common in *A. forsteri*.

Allosuckling occurs in pinnipeds, which can be costly behaviour to filial young and possibly females in *Arctocephalus forsteri*. Therefore, natural selection favours the rearing of one pup only. Consequently fostering is rare in this species and other otariids (Stirling, 1975; Georges *et al*., 1999; Haase, 2004). Fostering could have been attributable to many factors in this study but perhaps most likely recognition error. Milk stealing is less rare possibly because it appears not to be overly costly to the female and is beneficial to nutritionally stressed pups in *A. forsteri*.

This research coincided with the projects of Laura Boren, Sandra Negro and Dr. Abigail Caudron. Pup morphometry data and nursing times were kindly shared by Laura specifically to further investigate the cases of fostering and milk stealing. The pup and female samples were obtained by Abigail Caudron and Chris Muller in the frame of Abigail's research and the genotyping was carried out by Sandra.

Chapter 5: General Discussion

Otariid pinniped females are under strong selective pressure to recognise their offspring and discriminate between filial and non-filial young. The cyclic maternal feeding strategy employed by otariids means females frequently leave pups for long periods (<1-21 days; Gentry & Kooyman, 1986; Georges & Guinet, 2000) and must regularly relocate their offspring (Bowen, 1991). The extended duration of the mother-pup association in otariids compared with phocids also selects for well-developed long-term recognition (Riedman, 1990). This means the costs of failed reproduction may be greater for otariid females than for phocids that lose a pup because provisioning young over extended periods is energetically very costly (Clutton-Brock *et al*., 1989). Additionally, otariids usually breed in dense colonies and so females require recognition of pups in addition to using spatial cues to locate them, unlike some ice-breeding phocids that may rely mostly on spatial cues (Burns *et al*., 1972).

Recognition of mothers by pups is also important as starvation would likely result if a pup could not locate its mother (Mattlin, 1978; Trillmich, 1981; Charrier *et al*., 2001a; Insley, 2001). The costs of failed reunion are significantly greater for pups than for females, which is why our finding of pups that make more effort than females during reunion (Chapter 2) was expected. Nevertheless it is encouraging that our results are also in line with those from northern fur seals (*Callorhinus ursinus*; Insley, 2001) that also demonstrated that pups emit more calls than females during reunions.

Olfactory and vocal recognition behaviours exhibited by mothers and pups toward each other during the postpartum period allow rapid development and reinforcement of their recognition abilities, and consequently, the frequencies of these behaviours were observed to decrease over time (Chapter 2). Females reduced their effort in reunions over time, in terms of the number of calls emitted and the distance travelled, apparently coinciding with the increasing recognition and reunion abilities of pups. Surprisingly, reunions have been quantified in few pinniped species, therefore this research is valuable in contributing to the body of data on the recognition behaviours used in reunions between mothers and pups (Gisiner & Schusterman, 1991; Phillips, 1998; Insley, 2001; Dobson & Jouventin, 2003).

Vocal recognition of pups by females is facilitated by calls being stereotyped, with high variation between pups and a relatively low variation of calls within pups (Insley, 1992). The findings that New Zealand fur seal (*A. forsteri*) pup calls are individualistic, with combinations of acoustic features allowing a classification rate of 67% of calls to the correct caller (Chapter 3), support the results of the study by Page *et al*. (2002) on the same species and add to the many other studies on vocal individuality in other pinnipeds (Insley *et al*., 2003; Trillmich, 1981; Perry & Renouf, 1988; Insley, 1992; Job *et al*., 1995; Caudron, 1998; Fernandez-Juricic *et al*., 1999; McCulloch *et al*., 1999; Phillips & Stirling, 2000; Charrier *et al*., 2002b; Charrier *et al*., 2003c). This data, supported by behavioural observations, suggested that the vocal patterns of a pup plays a major role in a female's ability to locate them and that females discriminate between calls of filial and non-filial pups with high fidelity.

The apparently lower discrimination abilities of pups compared with females resulted in pups often responding vocally or approaching unrelated females (Chapter 2). However, as the costs of failed reunion may be high for pups, these behaviours may not represent a lack of discriminatory ability but may actually represent attempts to gain allomaternal care (Charrier *et al*., 2002a). The behaviour of pups engaged in milk stealing suggests that pups discriminate mothers from unrelated females, and will approach unrelated females to obtain additional nutrition despite the risk of being threatened (Chapter 4). However, it appears that *A. forsteri* females are less aggressive toward non-filial pups than females of many other species (Bowen, 1991; Harcourt, 1992; Insley, 2001; Phillips, 2003), as pups were bitten in only a small proportion of observations and none were wounded. This suggests that the costs of attempting milk stealing do not greatly outweigh the benefits in this species. If this is the case then the benefits of milk stealing may be high for pups in poor condition or those that are nutritionally stressed during maternal absence. Nevertheless, the provisioning of non-filial pups in addition to their own must be costly for females since lactation is energetically costly (Oftedal *et al*., 1987; Clutton-Brock *et al*., 1989; Boyd *et al*., 1995), therefore we would expect females to be threatening toward milk stealing pups. However, females may gain inclusive fitness by nursing non-filial, but related, pups, as predicted by kin selection theory (Hamilton, 1964). The recent expansion of *A. forsteri* from a bottleneck (Wilson, 1992) and the recent re-colonisation of the Ohau Point colony (Boren, 2001) suggests that genetic variability may be low, which may suggest that costs to allosuckling females may be reduced (Gemmell, 2003).

Pups may adopt other strategies in an attempt to gain allomaternal resources when under nutritional stress during maternal absence. In addition to responding more to unrelated females (Charrier *et al*., 2002a), they may also alter their vocal signatures (Perry & Renouf, 1988). In this study the findings that the variation in a frequency variable of *A. forsteri* pup calls decreased over time during maternal absence (Chapter 3) should be treated with caution as small sample size meant a test of low power. There were no differences found between calls emitted while mothers were present versus when they were absent. However, modifications of calls may occur due to changes in the state of motivation of the pup to feed and it is possible that the calling behaviour of females and other pups provides a greater motivation to nurse (Charrier *et al*., 2002a). Although anecdotal, such behaviour requires more extensive research.

The fostering of pups by females is rarer in otariids than in phocids (Stirling, 1975; Riedman, 1982), a trend that coincides with the general disparity of recognition abilities between the two families (Insley *et al*., 2003). Fostering was originally thought to be nonexistent in otariids because of the high-quality recognition system between mothers and pups (Marlow, 1972; Stirling, 1975; Mattlin, 1978). However, closer investigation in this study (Chapter 4) found upwards of 80 cases in nine species of otariids in the wild. The findings of four occurrences of fostering in *A. forsteri* are significant as they are among the first cases confirmed in this species and add to the relatively rare occurrence in otariid pinnipeds as compared to phocids.

Investigation of the two cases of long-term fostering or adoption of pups indicated that there are costs to filial pups of fostering females as resources are shared between two pups rather than one. One of the females did not appear to alter her foraging

cycle, suggesting there were no immediate costs of provisioning to two pups, however, if her filial pup did not survive, the consequences of fostering would be a reduction in reproductive success (Riedman, 1982). Given the costs to filial pups, in terms of reduced growth rate and potential decrease in survival (Georges *et al*., 1999; Haase, 2004) together with the possible costs to female reproductive success, fostering behaviour should be strongly selected against. However if there were other benefits of this behaviour, such as an increase in reproductive success by nursing non-filial, highly related pups, under kin selection theory (Hamilton, 1964) then such a behaviour may be favoured (Gemmell, 2003). The high relatedness between the foster pup X6 and the filial pup X7 supports this theory of the fostering of related pups to gain inclusive fitness. However, the extremely low frequency (0.44-1.3%) of fostering found in this study further suggests it is highly inauspicious behaviour for females to engage in and that selection pressures act against the occurrence of fostering. Given the limited duration of two of the fostering cases, it seems unlikely that there were high costs to the females, so there may have been benefits in these cases, such as an enhanced inclusive fitness (Hamilton, 1964). None of the fostering females had lost their own pup, contrary to the many cases of fostering reported in other species (Le Boeuf *et al*., 1972; Marlow, 1972; Schaeff *et al*., 1999; Harris *et al*., 2005; J. P. Y. Arnould, pers. comm.). It is possible that erroneous recognition developed between the fostering females and non-filial pups soon after birth (Rand, 1955; G. Hofmeyr, pers. comm.), which may explain the long-term adoption of two pups from when they were young. This was supported by observations of apparently mistaken females accepting non-filial pups for short periods of time (Chapter 2).

Future research

Despite a fair amount of quantitative research on aspects of recognition behaviour in wild pinnipeds, few other studies of this type have been carried out on the New Zealand fur seal (*Arctocephalus forsteri*; Page *et al*., 2002). Subsequent studies on mother-pup recognition systems in *A. forsteri* could utilise playback experiments to determine the exact timing of recognition ontogeny for both mother and pup (Charrier *et al*., 2001a). More research needs to be done to quantify the non-vocal cues used in reunion, those in the areas of visual, spatial and olfactory recognition (Phillips, 2003; Insley *et al*., 2003). Further experiments on vocal individuality would also be beneficial, utilising playbacks of modified vocalisations to confirm which acoustic features are used in recognition between *A. forsteri* mothers and pups (Charrier *et al*., 2002b).

As confirmed occurrences of fostering in otariids are few, more studies on fostering frequency are warranted. Genetic studies using non-invasive techniques (Caudron *et al*., in prep.) could provide accurate fostering frequencies. Genetic research could also investigate whether the Ohau Point colony has a low genetic variability and determine whether this is associated with fostering frequency by comparing with other colonies. Care must be taken to ensure disturbance is minimised, since that disturbance may affect the development of mother-pup recognition and may promote some cases of fostering. More work can be done to investigate the causes of fostering, especially studies on relatedness between females and fostered pups to further examine if kin selection influences fostering (Gemmell, 2003). The role of density and disturbance in promoting fostering (Fogden, 1968; Boness, 1990) should be investigated more thoroughly. Studies on recognition ontogeny could observe whether

females will accept non-filial pups and learn to recognise them before recognition of their filial pups takes place.

The idea of the use of alternative pup strategies under nutritional stress during maternal absence (Charrier *et al*., 2002a) should be investigated more thoroughly and in other pinniped species. Milk stealing should be quantified and modifications to other aspects of pup behaviour and to pup vocalisations should be further investigated. Here the body condition of pups should be taken into account because starved pups may alter their vocalisations more than healthy pups. Investigations could be made near the end of lactation when foraging trips are longer to allow trends in pup behaviour modifications correlated with nutritional stress to be observed more clearly.

Conclusion

My research on the New Zealand fur seal, *Arctocephalus forsteri*, demonstrates the well-developed recognition abilities between mothers and pups of another otariid species to add profundity to other studies that quantified these behaviours (Gisiner & Schusterman, 1991; Insley, 2001; Dobson & Jouventin, 2003; Phillips, 2003). The rare and exciting discovery of allosuckling, along with those in other otariid species (Lunn, 1992; Georges *et al*., 1999; Childerhouse & Gales, 2001; Gemmell, 2003; Haase, 2004; Porter & Trites, 2004; Harris *et al*., 2005), indicates that despite the recognition system in place between mothers and pups and the costs involved, fostering does occur. This suggests that some recognition errors may occur under certain circumstances, such as disturbance (Rand, 1955; Fogden, 1968), or perhaps there are benefits provided to the fostering female in some cases, such as those of

inclusive fitness (Hamilton, 1964) if she is fostering a related pup (Gemmell, 2003). These discoveries provide the background for further investigations of the causes of fostering in *A. forsteri*.

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